

EAST AFRICAN MAMMALS

An Atlas of Evolution in Africa

Volume IIID

Jonathan Kingdon



Academic Press



For fifteen years Jonathan Kingdon studied and portrayed the wildlife of Kenya, Uganda and Tanzania. Since 1971 his work has been published in a series that has gained international acclaim as one of the most remarkable zoogeographical studies of our time — *East African Mammals*. In successive volumes the primates, small mammals, and latterly, large mammals, have been subjected to the exhaustive scrutiny of a dedicated observer. Details of behaviour and anatomy undetected by the camera have been captured in exquisite and vital line drawings and sketches. A wealth of information on physiology, distribution, social systems, habitat, ecology and evolution has been encapsulated in a penetrating and commanding text. Taken individually, the volumes of *East African Mammals* provide the most comprehensive guides available for their particular subjects: taken together they make up a treatise of immeasurable value, which culminates in this two-part volume on the bovids.

In considering over 40 species of East African bovids, Jonathan Kingdon offers not only new information but also a new approach to this group of mammals. Thus original information on, for example, dwarf and hippotragine antelopes, forest duikers, bongo and hartebeest is set in the context of a fresh approach to the bovid family as a whole, which is presented for the first time as a single evolutionary radiation. In addition, the confusing area of bovid taxonomy is re-appraised, and a simple classification of subfamilies and tribes based on recent ecological and palaeontological research is proposed. As in previous volumes, there is considerable emphasis on the relationship between form and function; body architecture and size, horn shape, coat pattern and tooth structure are some of the aspects that are discussed in a broad comparative, ecological and evolutionary context. Further understanding of bovid ecology and evolution should have far-reaching effects on animal husbandry and range management in Africa, at present largely based on practices developed in more temperate climates.

Throughout the text Jonathan Kingdon displays a rare ability to combine a thorough and critical exposition with an intuitive understanding of his subject, perhaps best displayed in his beautiful and sensitive drawings. In all the volumes of *East African Mammals* his concern for the fauna of this tropical region is paramount. As the ancient links between Man and animal are broken down, and Man becomes careless of his environment and the multiplicity of species it fosters, the mammals of East Africa, and indeed the entire continent, are threatened. Understanding can only be restored through knowledge of the evolution, biology and ecology — and hence needs — of these species: few books are more likely to pave the way than *East African Mammals*.

"I have nothing but praise for this book . . . It is indispensable, both for our knowledge of the East African mammalian fauna, its habits and its geological history, and also for indicating what gaps in our knowledge, especially of their behaviour, remain to be filled. I commend it to all serious students of African ecology, both for the beauty of its illustrations and for its biological thoroughness."

Sir Julian Huxley
from a review of Volume I

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EAST
AFRICAN MAMMALS

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An Atlas of Evolution in Africa

Volume III Part D (Bovids)



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Contents

BOVIDS, HORNED UNGULATES (BOVIDAE) continued

GAZELLINE ANTELOPES (Antilopini)	394
Thomson's gazelle, Tommy, <i>Gazella thomsoni</i>	402
Grant's gazelle, <i>Gazella granti</i>	414
Soemmering's gazelle, <i>Gazella soemmeringii</i>	422
Gerenuk, <i>Litocranius walleri</i>	426

ALCELAPHINES (Alcelaphini)	438
Impala, <i>Aepyceros melampus</i>	460
Hirola, Hunter's hartebeest, <i>Beatragus hunteri</i>	476
Topi, Tiang, Damalisc, Bastard hartebeest, <i>Damaliscus lunatus</i>	484
Hartebeest, Kongoni, <i>Alcelaphus buselaphus</i>	502
Gnu, Wildebeest, <i>Connochaetes taurinus</i>	524

HORSE-LIKE ANTELOPES, HIPPOTRAGINES (Hippotragini)	538
Sable antelope, <i>Hippotragus niger</i>	554
Horse antelope, Roan antelope, <i>Hippotragus equinus</i>	568
Oryx, <i>Oryx gazella</i>	578

SHEEP AND GOATS, CAPRINES (Caprini)	588
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Appendix I: Conservation	592
Appendix II: Management of Mammals in Captivity	608
Appendix III: Disease and Parasites	633
Appendix IV: Exploitation	639
Bibliography	643
Checklist of Species with Authorities	705
Gazetteer	711
Systematic Index	715
Subject Index	723



Gazelline Antelopes

Antilopini

Genera	Species
<i>Gazella</i>	<i>Gazella thomsoni</i>
	<i>Gazella granti</i>
	<i>Gazella soemmerringii</i>
<i>Litocranius</i>	<i>Litocranius walleri</i>

Contemporary species of gazelline antelopes have specialized in long limbs and adaptation to drought. Most gazelle species are smallish and lightly built but the members of the *G. granti* (or *Nanger*) group are taller. Their relatively primitive dentition and skull structure imply an archaic status that has been confirmed by the appearance of a gazelle-like fossil in the 12 to 14 million-year-old deposit at Fort Ternan (Gentry, 1970a) and still earlier at Jebel Zelten (16 million years) (Thomas, 1979b).



Strong development of the senses of sight and hearing are reflected in the animal's behaviour, in large eyes, orbits, ears and auditory bullae. Faculties well suited to a vulnerable existence in relatively open habitats and matched by an exceptional alertness to sounds and movement.

In the males of some of the smaller species preorbital glands are used for marking territories and there is obviously a strong olfactory dimension to their world. However, the larger species have rudimentary face glands and do not attempt to mark out their large and periodically deserted home ranges.

There has been a very early divergence within the Antilopini with respect to the nasal area. Nasal bones and the olfactory region have seen phylogenetic diminutions in size and volume, a trend that reaches its extreme

Above and opposite: *Gazella granti*, female.

in *Saiga*, an antelope with a dik-dik-like nose, which Gentry (1978a) places with the Antilopini.

Freeing the lower muzzle from the constriction of a nasal tube is probably correlated with increasing the flexibility of the nostrils and improving temperature regulation. It is significant that this development should occur in the genus which has adapted best to extremes of heat. Indeed a major factor in the survival of gazelles must be their physiological tolerance of heat. Their conservative and unspecialized teeth and diets can have little to do with it and they are not generally successful in cooler, moister habitats.

In another genus of Antilopini, *Antidorcas*, long nasals roof over a tapered but well-developed olfactory chamber. Fossils belonging to this genus occur in Pliocene and Pleistocene deposits in North, South and East Africa and this appears to have been the pre-eminent antilopine type for much of the Pleistocene. Today it is represented by the springbok, which is restricted to South Africa. Although reasonably resistant to heat and drought in the Kalahari there is no evidence for tolerances comparable with those of the Sahara or Somali Gazelles. The existence of several species, their abundance in fossil deposits over several million years and their continent-long distribution suggests an ecological range and success that makes a sorry contrast with the springboks' relict status today. If a capacity to cope with tough diets was any consideration, *Gazella* should be inferior to *Antidorcas* (it actually proved to be so in South Africa) because the latter has higher-crowned teeth and a deeper mandibular ramus; (hearing is less important if the smaller size of bulla and pinna are anything to go by).

It seems likely therefore that gazelles, by virtue of their special physiology are the most successful survivors of a larger bovid group that was formerly very successful in a wide range of habitats, although the group's emergence in the first place was obviously the product of an adaptation to drier climates and more open country.

Other survivors are even more specialized. The giraffe-antelope or gerenuk, *Litocranius*, and the dibitag, *Ammodorcas*, have both followed the antilopine trend of lengthening the limbs and neck but have carried this trait to extremes. The body size has increased with the huge upward extension of their feeding zone, but the diet, teeth and stomach structure have remained very conservative.

In the contemporary spectrum of bovids, the antilopine niche can be described as that of conservative feeders that pick a living in dry or very dry areas where rainfall is unreliable, resources are dispersed and an animal's physiology is severely challenged. The obvious challenge of adapting to tougher, less nutritious grasses in the diet was taken on by the *Antidorcas* branch. Movement into a new dietary niche, with vast expansion in the resource base eventually permitted increases in size and diversity, which transformed the antidorcine lineage—they became what we term alcelaphines. Further discussion of this is therefore reserved for another profile.

The Antilopini are one of the few groups of antelopes that have been outstandingly successful outside Africa. They had probably already diversified before adapting to local extremes of climate (as *Panthalops* has done in Tibet and *Saiga* in Central Asia), their evolution is therefore by no means exclusively African. The genus *Gazella* has an Asian branch, the



Gerenuk, *Litocranius*.

subgenus *Procapra*, but the main theatre of their evolution is likely to have been the arid regions of North and North-East Africa and its wayward appendage, Arabia.

The radiation of *Gazella*, even within Africa is of long standing and the major species groups have very distinctive adaptations. Groves (1969) split the smaller species in two subgenera and Lange (1971) treated the larger species, *granti*, *soemmeringii* and *dama* as the subgenus *Nanger*, and he regarded *granti* as the most evolved of these, partly on the basis of horn shape and coat pattern. Horn size can be related to body size, height, weight and to population density. The upper limits are reached by *G. granti*, which lives at higher densities in relatively richer environments than either *dama* or *soemmeringii*. Significantly this species has the longest and heaviest horns, with a record length of 80.6 cm and an average of 50 cm. Such length puts enormous stress upon the skull and it should be appreciated that the horn has retained a primitive bovid anchorage above the orbit and that the stresses of clashing must travel across a cantilever instead of being absorbed directly on to the heavily reinforced cranium. The Saharan *G. dama* has not elaborated its horns to anything like the same degree, a reflection perhaps of lower densities and wider spacing of territories but also of the handicap they impose under harsher conditions. The smaller species provide good examples of early stages in the phylogeny of horns—they represent limited elaborations of a simple spike.

The advanced status of *G. granti* is not only manifested in its horns and size. The environmental demands put upon a larger animal differ from those put on a smaller and Taylor (1972) investigating the water balance of two East African gazelles under laboratory conditions found the paradoxical situation of *G. granti* requiring one-third more water per kg of body weight than *G. thomsoni*. Subjecting the animals to intense heat, Taylor found *G. granti* allowed its body temperature to exceed air temperature, whereas *G. thomsoni* relied on evaporation to keep its body temperature down, so that when the air was 45°C its blood was 42.3°C. At the same external temperature, *G. granti* had a body temperature of 46.5°C. This temperature is too high for the brain so the blood is put through a cooler before it reaches the brain, (the mechanism for this is similar to that of the dik-dik and is described on p. 249). The problem of the extra water needed by *G. granti* for nasal evaporation is solved through the expedient of feeding at night. Taylor found that in spite of the dew point being seldom reached in the sub-desert, there is enough humidity for the leaves of *Disperma* (the gazelles' principal browse during drought) to pick up 40% water after eight hours of darkness. A stomach filled before dawn would therefore provide the one to two litres of water that are needed by the gazelle.

The smaller size of *G. thomsoni* influences densities and Estes (1967) was able to compare the two species in the 100 sq. miles Ngorongoro crater where there were approximately 3,500 *G. thomsoni* to 1,500 *G. granti*. Estes found that predation played a very important part in the regulation of animal numbers in the crater. Hyaenas generally have a one in three chance of running a gazelle down (Kruuk, 1972). Jackals take large numbers of the young (in spite of the mother's efforts to distract or butt them) and Brooks (1961b) thought they might be the most effective predator of *G. thomsoni*.



over the whole of their range. Cheetah are more dependent on gazelles than any other prey, comprising over 90% of their kills on Serengeti (see Vol. IIIA, pp. 398—402). Around Seronera the leopards living in the river courses manage to kill numerous *G. thomsoni* because of the weir effect of the woodlands, against which the plain-loving gazelle populations press, bringing them within the range of the leopards' stalks and rushes.

Adult gazelles, particularly territorial males, are especially vulnerable to wild dogs (Estes, 1967). Due to their rather thorough foraging methods, baboons are also a hazard during the birth season and many young are taken wherever baboons are numerous. Pythons have been recorded swallowing adult gazelles (although one, unable to crush the horns of a male, was seen to disgorge it).

Beaton (1949) described a secretary bird attacking and carrying off a newborn gazelle; martial eagles and lappet-faced vultures also kill the young.

The selective effects of predation also seem to apply to disease. Schiemann (in Kruuk, 1972) noted two-and-a-half as many males as females dying of disease. Sarcoptic mange becomes particularly common and severe at the end of the dry season, when many territorial males are likely to be suffering from malnutrition.



Right: female *Gazella granti*. Opposite page: female *Gazella thomsoni*.

Greater independence from water in Grant's gazelle allows it to use arid areas that are closed to Thomson's gazelle, this is reflected in the former's greater overall distribution in East Africa. Being water-dependent *G. thomsoni* overcomes part of its disability by being more migratory than *G. granti* and is specially well-adapted to take advantage of regrowth after burns, moving considerable distances over short periods of time to congregate on seasonal pastures, often in very large numbers (Brooks, 1961).

The social implications of these differences are that Thompson's gazelle have remarkably open associations in which individuals come and go without difficulty (Walther, 1968). In Ngorongoro, Estes (1967) recorded that the spacing of temporary groups (averaging about 23 animals) corresponded with the spacing of territories in that they tended to be 100—200 m apart.

Population density and body size also influence the behaviour of gazelles. Territorial males of Thomson's gazelle clash with fewer preliminaries, with greater frequency but more briefly. Grant's rely more on display, the older males in particular being slow to fight, but when they do fight the contest is more prolonged and intense. Root (personal communication) has watched and filmed fighting males of *G. granti* that were so preoccupied that a cheetah had to come up and bat one on the hindquarters before they broke off and fled, whereupon one was quickly dispatched by the cheetah. Such observations illustrate the disadvantages of frequent fighting and imply benefits for their partial or progressive replacement by ritualized display.

The ritualization of common postures can take on opposite meanings for very closely related species (see Vol. I, p. 203). This has occurred with stereotyped pseudo-grazing, which Walther (1968) called "excitement grazing". In Grant's gazelle Walther found this action was only performed by an inferior animal, never a dominant one, whereas it is more characteristic of powerful territorial males in Thomson's gazelle and appears to be a mechanism by which animals can take one another's measure. It is protracted

and might be regarded as a display of very low intensity, in which case, as a common prelude to a fight, it may be the equivalent of more ostentatious displays that precede a confrontation between Grant's gazelle males (p. 420).

The superficial similarities between Grant's gazelle and Thomson's gazelle have provoked some discussion about isolating mechanisms in the areas of sympatry. As the detailed drawings demonstrate, the differences in morphology are much more substantial than is generally appreciated and are, as Estes remarked (1967) adequate to bar interbreeding. The employment of facial glands by Thomson's gazelle, while they are vestigial in Grant's, can only serve to emphasize the different modes of communication that are used by the two species. The differences in pattern, although employing similar tones and markings, are formulated into uniquely distinctive signals.

Observation of the behaviour of gazelles has suggested that the signal value of their highly conspicuous white and black flash patterns overrides the disadvantages of increased exposure to predators that goes with it. However, all species have infantile coats which are cryptic and the fawn backs and necks of adults are a reminder of their early vulnerability before long legs and sociability emancipated them. The limitation of a prolonged lying-up phase, like the teeth and other aspects of their biology is typical of a very conservative antelope. It is one of many suggestions that the gazelline antelopes' make-up is a peculiar mosaic of archaic, advanced and specialized features.





Thomson's gazelle, Tommy (*Gazella thomsoni*)

Thomson's Gazelle, Tommy (*Gazella thomsoni*)

Family

Bovidae

Order

Artiodactyla

Local names

Swala tomi (Kiswahili), Sasunga (Kinyaturu), Thwara (Kikuyu), Mpefe (Kirangi), Enkopera (Masai, Samburu), Nindala (Kijita), Nauren, Katebe (Turkana).

Measurements head and body

89—107 cm

height

62 (58—70) cm

tail

19—26 cm

weight

20—25 (17—28.7) kg males

16—21 (13—23.5) kg females

horns

25—43 cm

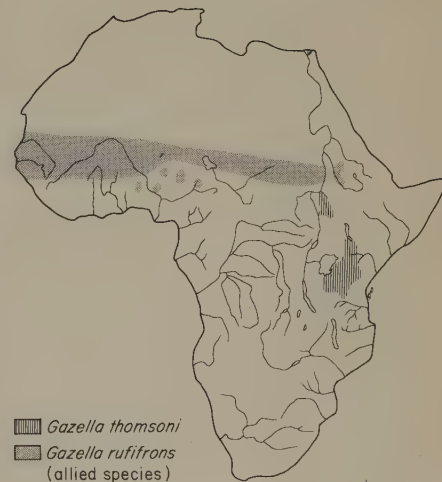
(Note: There is a north to south decrease in average measurements.)

Races

<i>Gazella thomsoni thomsoni</i>	predominantly east of Rift Valley
<i>Gazella thomsoni nasalis</i>	predominantly west of Rift Valley

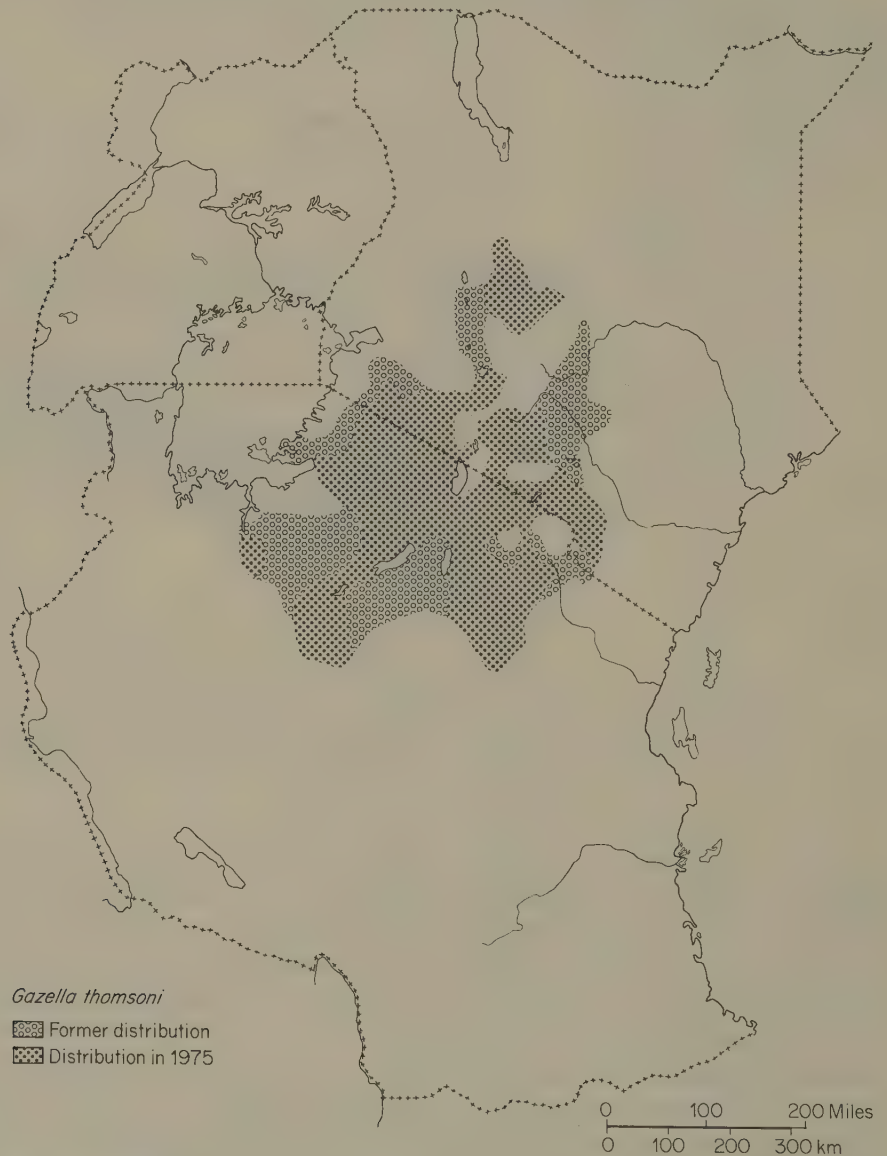
Thomson's gazelle is a compact little gazelle with a cinnamon back and a bold black flank stripe beneath a pale buff band; the underparts are white. The face has a black eye stripe, the nose a dark marking and the forehead a light patch, all of which are subject to individual variation (illustrated in Walther, 1973). The males' horns are heavily annulated. The females have smooth short horns or none at all.

There is a closely related population in the southern Sudan which is sometimes treated as separate species (*albonotata*). A related species *G. rufifrons* from the southern margins of the Sahara is adapted to drier conditions than *thomsoni*, which is restricted to the plains of the East African plateau in southern Kenya and northern Tanzania. Taylor (1972) has shown how *G. thomsoni* is less adapted to truly arid conditions than *G. granti* because it relies on evaporative cooling by panting and it keeps its body heat several degrees below the outside temperature, whereas *G. granti* adopts a different strategy. Hofmann (1973) notes the relatively small salivary



glands and food preferences as possible limiting factors. Nonetheless, like all gazelles the tommy is more drought-resistant than most ungulates.

They depend upon larger animals to graze and trample the range, or on fires to burn off the tall grass cover. They are therefore closely associated with cattle or the larger ungulates, gnu and zebra. Principally grazers, they also browse off shrubs particularly in the more wooded southern areas of their range and during the dry season, at which time they also eat a lot of seeds, notably of *Balanites*, *Boscia*, *Acacia pallens*, *Acacia verugera*, *Solanum renschii* and *Sida* spp. (Burt, 1929; Bell, 1969).



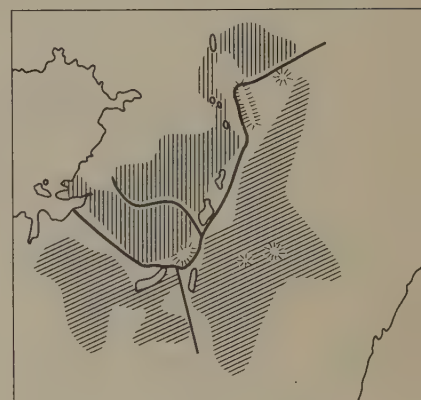
In the Serengeti Gwynne and Bell (1968) found that tommy eat lush green grass in the rains but in the dry season eat only 61% grass (selecting for sheaths rather than stems) and turned more to fruit and leaf of dicotyledons. Stewart and Stewart (1970) found a similar seasonal pattern and they identified *Cynodon* species, *Themeda* and *Harpachne schimperi* as favoured grasses.

During the wet season when grass is growing very fast, it is difficult for the species adapted to short grass to cope with the growth, and tommyes tend to be concentrated at this time. With the first rains they often move into areas that were heavily used by large water-dependent ungulates during the dry season. This reversal of pattern is interesting, with the larger ungulates dispersing just as the gazelles concentrate on the ground they have vacated, which is usually quite bare except for the tiny shoots that attract the gazelles. The principal wet season refuges have well-drained soils and are generally treeless. They are estimated by Brooks (1961b) to constitute no more than 10% of their annual range. These concentration areas are also traditional calving areas. In June the plains and cotton soil *mbugas* are drying out and are attracting the larger grazers. It is also the month when the grass fires start, releasing large areas of fresh green grazing. The gazelles follow in the wake of the gnu and the zebra at this time and there is a general dispersal of the tommyes out over the plains. This is accompanied by the onset of territorial behaviour, so that large areas are scattered with males, among which wander small groups of females and young.

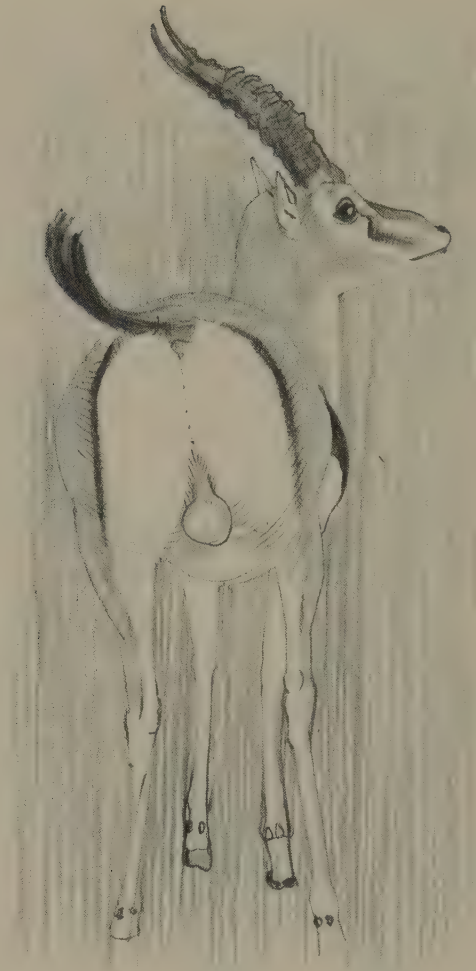
Brooks has suggested that local populations exist within a definable ecosystem and in spite of close geographical contiguity maintain a high level of genetic distinctiveness (see margin). He found evidence for this in measurable and consistent physical differences between neighbouring populations.

The distinctness of regional populations must certainly be reinforced by, if not originate in, the social system. In Serengeti, Walther (1973) discovered that a functional unit of females and their offspring maintained a temporary but distinct home range of 1.5 sq. km for several months in spite of the fact that the animals were part of a migratory population. This herd had a very definite daily circuit which did not impinge upon similar circuits by neighbouring herds except that every evening there was what Walther called a "big meeting" of two herds, in which there was an exchange of members, with the result that the numbers of the study herd fluctuated from 50 to 200.

Here is an extraordinarily flexible system; migratory animals without lasting ties between individuals space themselves out into a loose mosaic of overlapping female herds. Yet in spite of changing membership each of these units establishes and sustains a regular routine within definite boundaries. These are not group territories because there is continuous exchange, and changing membership effectively prohibits the development of a hierarchy. Common activity cycles cannot be the only cause for the relatively synchronized and uniform behaviour of a group, and Walther (1973) saw group activity being co-ordinated through two social factors, contagion and aggression. In the first case, members of a group simply tended to imitate one another; in the second, threats from active animals towards others that were resting, grazing or even moving speeded up shifts from one group activity to another. The latter has no implication of a dominance system and it is interesting that male coercion appears to have a minimal influence on the movements and groupings of females as the nursery herd passes through a succession of territories as well as visiting

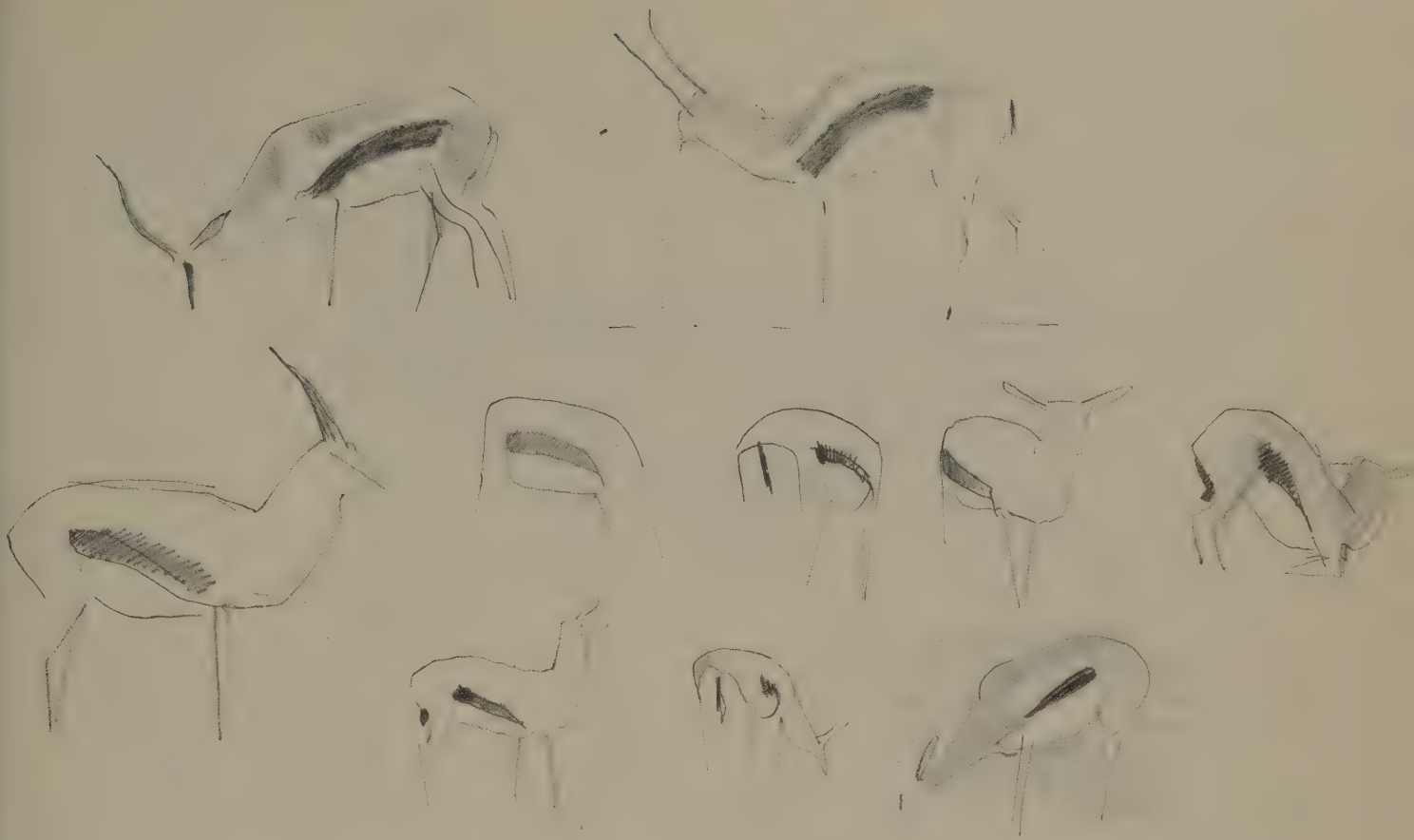


Sub-populations recognized by Brooks (1961) within the two sub-species of Thomson's gazelle.



bachelor areas in a single day (Walther, 1973). The males are preoccupied with defending their territories from other males and with identifying and courting single oestrous females.

Mild aggression involving horn tilts and herding by non-territorial males may help promote group activity and synchronize movements (Walther, 1978), but the rarity of obvious sources of leadership or dominance emphasizes that the gazelles must rely on a continuous awareness of one another to co-ordinate their activity. Their highly distinctive colouring must serve this purpose very well and it is interesting that stotting and pronking behaviour is particularly well developed in this species. As in many other antelopes it is the juveniles and subadults that most frequently break into a bouncy self-advertising gait, or sprint around the herd in a circle. Because the behaviour is seen in response to disturbance it is often assumed that it is directed at predators but Walther (1973) noted that "running games" occur most frequently in the early morning and in the evening and most particularly when big herds meet. He pointed out that the behaviour is contagious in effect but that each animal runs or bounces along on its own.



Noting that there is a correspondence with low temperatures and daylight, he assumed that there is an important endogenous component. I have discussed the bovids' ritualized gaits earlier (p. 37) and I have suggested that their primary purpose is to force or reinforce social responses in conspecifics by drawing attention to a peculiar activity. This is directed towards different ends in different species but in the gazelles a most important function might be co-ordination of activity, since it is a visual signalling system that apparently holds them together. The functional link between visual communication and stotting would explain why Walther never saw "running games" at night.

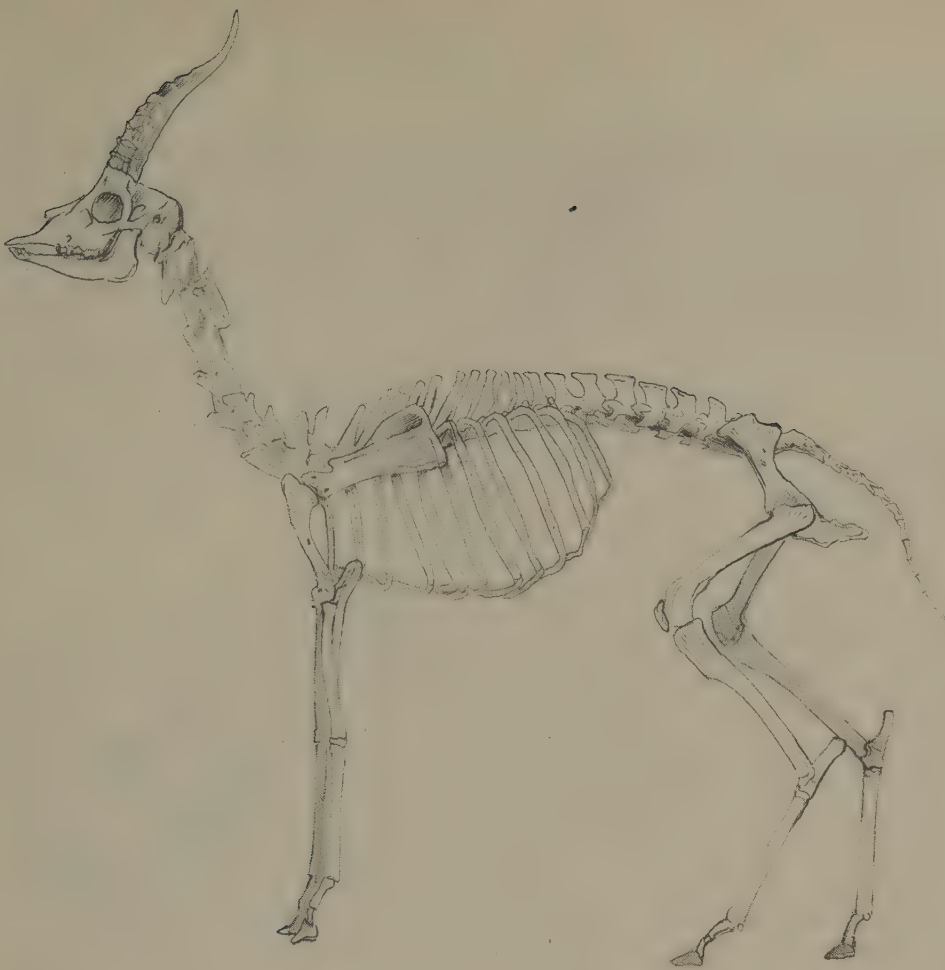
Females maintain their regular cycle of activity and movement in the face of frequent excitements and disturbances, regrouping after repeated scatterings. Although stotting may be triggered off by an excitement such as predators or a meeting with strange animals or even by a cool breeze, its very conspicuousness must serve to keep the bouncing animal in view of its fellows and so avoid breaking contact. There is almost continuous wagging of the tail, which seems to signify mild excitement: for instance, it accompanies the first deliberate movements away from any distant source of threat. A nearer approach by an observer may be followed by an alert posture, foreleg-stamping and, just before flight, a violent shudder of the dermal muscles of the flanks, which has the effect of flashing the black and white side stripe. These actions affect neighbouring gazelles, which become alert and may even draw nearer one another in the face of danger, only to scatter widely once they start running.



In the face of mild alarm, young animals raise their tail and display their rumps; Brooks (1961b) thought that these younger animals flare the white rump patch more effectively than adults. Although commonly displayed in the presence of predators, this behaviour is probably related in the first place to members of their own species, possibly as an appeasement signal.



Like the Grant's gazelle, tommy males have exaggerated urination-defaecation postures and they sometimes paw the soil before excretion. Tommies are most active in the earlier part of the morning and in the afternoon and evening. They like to rest, if possible in shade, during the heat of the day, lying down in a posture that hides their markings well. Sometimes, when the sun is very strong, many hundreds of gazelles face in the same direction, all with their backs to the sun.



The social structure of the tommy herd is probably subject to considerable variation. Some populations disperse from dense non-territorial concentration areas in the rains into a wider dry season range, where the males adopt and defend their territories. In the Ngorongoro crater, Estes (1967) found territorial males about 22—300 m apart. Female groups circulated within a mosaic of territories in more numerous and closely spaced groups. Whenever concentrations formed, they tended to be split up by the territorial males. Non-territorial males gathered together in small peripheral groups and avoided the territories. In both classes the herds averaged between five and fifty. Walther (1968) contended that peripheral male or juvenile groups also have a marked home range but that this is not defended.

The territories of tommy males are characterized by favourite resting spots and grazing areas and by about a dozen dung deposits, usually placed on patches of bare soil. They are also marked out regularly by the male's preorbital gland secretion. Grass stems, 30—40 cm high are inserted into the gland and the little gobs of secretion are renewed daily. Estes (1967) found marked stems spaced between 4—8 m apart and he counted 68 to 153 deposits within one territory.

Since most tommy populations make seasonal shifts, these territories are relinquished when the gazelles move. Nonetheless a male's defence of his land is intense; occasionally bachelor herds are allowed to graze through, but other males are generally challenged or pursued vigorously. For many weeks after the females have abandoned an area, a scattering of lonely territorials will stay on their grounds. Territorial behaviour in Thomson's

gazelle is conspicuous, and Walther (1973) noted daily peaks in aggressive behaviour and he thought that territorials actively sought out fighting contests. After a reciprocal threatening tilt of the horns both animals leap forward towards one another with widely splayed forelegs, bleating and occasionally flickering the side stripe. They lower their heads to the ground

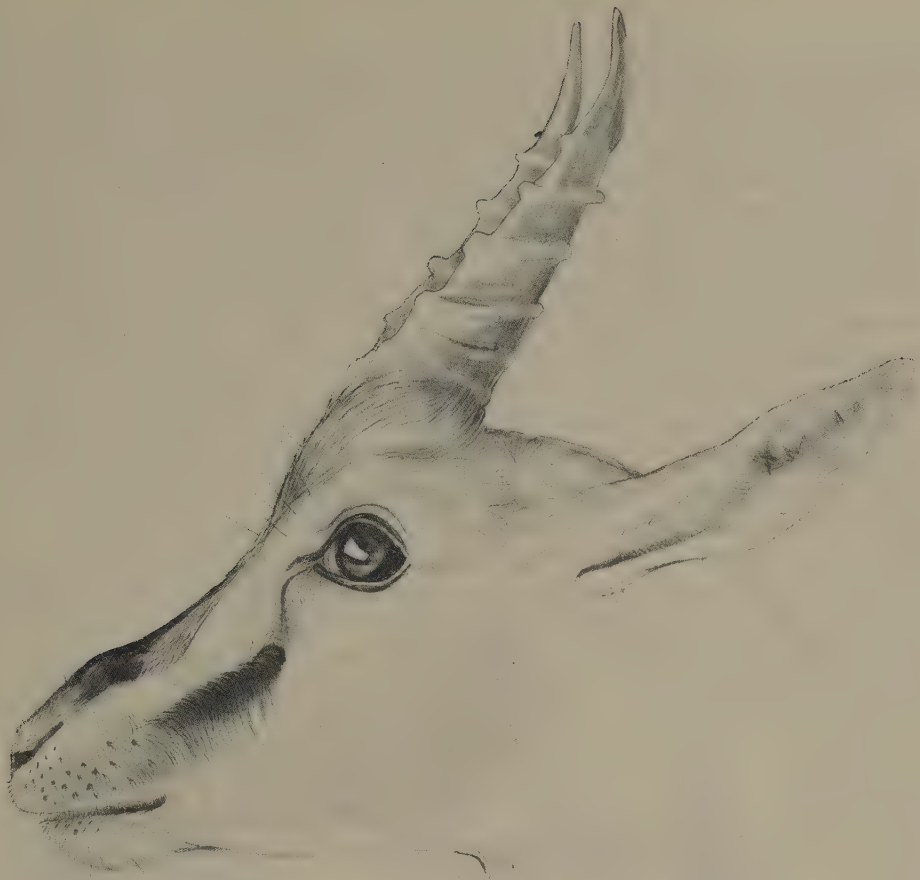


and clash their horns, only to disengage and leap back. This may be repeated, or the horn clashes may be interspersed with sessions of self-grooming (particularly on the shoulder), scratching with the hindleg or grazing. The grazing position is similar to the fighting posture and it is possible that when two rival males graze side by side along their mutual boundary and in between bouts of fighting this activity is equivalent to a ritualized challenge display in function. In fact preliminaries are brief and the males close in on one another with horns advanced. Estes (1967) remarked that the configuration of the tommies' horns and their method of limited parrying makes it so unlikely that they will harm one another that the need for ritualized threats is reduced. Nonetheless, a thrust with the point is dangerous and sharp wrenches break off horn tips. Old animals frequently have broken horns, which are further worn by abrasion against the earth.

Thomson's gazelles breed twice a year. The females come into oestrus within a month of giving birth, so their birth peaks are followed by or coincide with mating peaks; a gestation between five and six months gives this pattern a cyclic regularity with the main birth peaks during relatively dry periods after the rains in January—February and again in July. Hvidberg, Hansen and de Vos (1971) noted that birth peaks are more pronounced in localities with typical rainy seasons. A male separates an oestrous female and tends her with a curiously mechanical sounding bleat, uttered with the head stretched forward and the nose periodically nodding or swooping upwards. Like many other antelopes, they kick out with the forelegs under the female's belly but tommies are peculiar in taking a series of rapid steps on still-held forelegs called the "drumroll" by Leuthold (1977b). In mounting the male rises on his hindlegs and can walk in this position without support, a necessary feat as the female does not stand still. Penetration and ejaculation is very rapid. In spite of the male's detaining tactics, oestrous females move from territory to territory, where they may be served by several males.

Hvidberg, Hansen and de Vos (1971) found males reproductively active at one-year-old but not territorial before two. Females had their first calf at about 18 months of age. Young were always carried in the right horn of the uterus and weighed 2,200—3,000 g at birth.

Walther (1968) reported that the females choose to bed their fawns down in the no-man's-land between territories, where they may be less disturbed.



The young hide successfully in remarkably open country. Their tawny colouring and complete immobility make them very difficult to see. Mothers visit them several times a day. Brooks (1961b) reported a mother nudging the young before leaving and the fawn responding by lying down.

Mothers of newly-born young will attack jackals and baboons and Estes (1967) noted mothers combining forces against jackals. Males never assist in the protection of the young nor will they defend an adult, and two male tommies reportedly chasing off a pair of jackals that were in pursuit of a female were probably compelled more by direct competition for the female than by any protective impulse.

The young grow rapidly and are weaned at about two months. By the time they are one-year-old they are effectively adults, although they only weigh about 16 kg and have relatively short, slender horns.

Predation on the young is very heavy and many predators feed on nothing else during the calving peaks. The rate of survival must vary greatly from year to year, but Schaller (1972b) established that 35% of the population at Seronera were fawns below the age of one year.

The age-class distribution of a predator-controlled and heavily cropped population on a Kenya estate was compared by Hvidberg, Hansen and de Vos (1971) with Brooks' (1961) data from wild populations in Tanzania.

The effect of heavy predation on wild stocks was evident in the vastly increased survival of young gazelles on the ranch.

Schaller (1972) found that the resident lions around Seronera feed almost entirely on gazelles after gnu and zebra have passed. Estes and Goddard (1967) and Kruuk (1972) recorded males as being up to three times more susceptible than females to all the major predators (except cheetah). Both bachelor groups congregating near the river beds and inattentive or limping territorials were highly vulnerable. The cheetah, although non-selective as to age or sex class, is nonetheless very persistent in following one gazelle only, ignoring the others as it races its prey down in a short fast chase in which the gazelle runs up to 80 kph. Of the chases watched by Schaller 70% were successful and it is evident that the cheetah has adapted its hunting behaviour to counteract the gazelle's escape tactics. That these work more effectively against lions is shown by Schaller's observations and records of 417 hunts. When the gazelle was in an aggregation of more than 75, or when it was on its own, a third of the hunts ended in a gazelle being killed, but it is significant that in groups smaller than this the chances of the gazelle escaping rose to more than three to one. Tommies present a dull brown



back as they kick off, but as their forelegs come down there is a white flash of buttocks, which disappears as suddenly as it appears; in rapid zig-zags to the right and left there are often flashes of black and white all round a pursuing lion. Schaller did in fact see a tommy jump right over an apparently bewildered hunting lioness.

The group-hunting of gazelles by wild dogs and hyaenas is more effective than the lion's stalk or ambush. The wild dogs have a fifty-fifty chance of success after adult gazelles (Schaller, 1972b), although they tend to chase several independently or to switch their attention from one gazelle to another as the hunt proceeds. In wet muddy weather or on very dark nights, tommy are helpless and Kruuk (1972) found over a hundred killed by hyaenas on such a night during the rains.

Tommy often persist on ranches and farmland long after other species have been eliminated. Because of heavy parasite loads carcasses have not been fully exploited in cropping schemes but large numbers are shot or snared for the pot. Although there has been no very extensive contraction of range the animal has, in recent years, become rarer in many localities.



**Grant's
Gazelle**
(*Gazella granti*)

Family
Order
Local names

Bovidae
Artiodactyla

Swala granti (Kiswahili), Lala (Kisukuma),
Hidi (Kiliangulu), Kalonga (Kamba),
Lakwedde (Lwo), Akete (Turkana), Agete
(Ateso, Karamojong), Engoilii, Enaragas
(Masai), Nkolii (Samburu).

Grant's Gazelle (*Gazella granti*)

Measurements head and body

155—166 cm males

140—150 cm females

height

84—91.5 cm males

75—83 cm females

tail

20—28 cm

weight

65 (58—81.5) kg males

45 (38—67) kg females

horns

45—80.5 cm

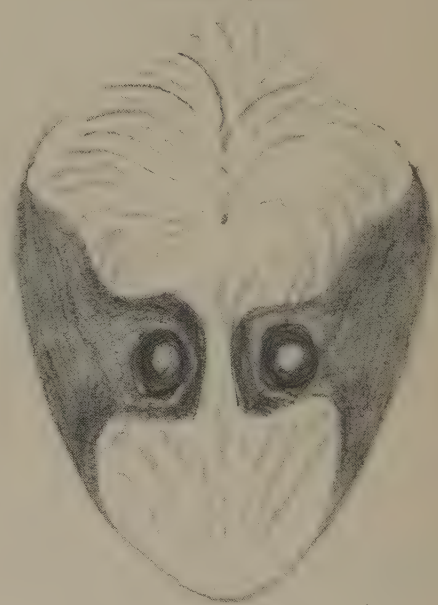
Races

<i>Gazella granti granti</i>	Tanzania and South Kenya
<i>Gazella granti robertsi</i>	Lake Victoria hinterland
<i>Gazella granti brighti</i>	Uganda and West Kenya
<i>Gazella granti petersi</i>	North-East Kenya

A large pale gazelle with long legs and horns, Grant's gazelle is recognizable from a rectangular white shape on the hindquarters and a sharply contrasting black stripe down the thigh, a pattern that can be tentatively interpreted in the light of the animal's life history.

Light coloured fur around a dark anal area is not unusual in antelopes but females of Grant's gazelle exhibit a particularly strong contrast between the vertical strip of black perineal skin and the white buttocks, which are sleek and short-haired. Below this stripe black skin also surrounds the teats and contrasts strongly with the white fur of the udders. These are visual foci for the fawn's attraction to its mother from the very earliest age. First, as a source of milk and later, when the young animal is mobile, the perineal stripe becomes a beacon to follow. Maintaining visual contact is made easier by side-to-side switching of the tail and by the white rump. In spite of the hair's being short and snowy-white, the depression of the tail and the bulge of the buttock muscles sometimes obscures the visibility of the black perineum. Vertical black lines down each thigh resemble the perineal stripe rather closely and their tops terminate in line with the anus. Above, the horizon of the tail extends into a small white patch which enhances the mimicry. Because the true perineum is only visible from directly behind and at relatively close quarters this device would seem to ensure that the signal can be seen from a greater distance even from a lateral viewpoint. The significance of this is unlikely to be limited to the mother-young relationship.

Mammary gland.



The only sustained relationship in gazelle society is that of a mother and her most recent offspring but with the exception of females that have recently calved and territorial males, *G. granti* are gregarious. Walther (1972b) has listed the various social groupings and both he and Estes (1967) found that individual membership was temporary. The initial stimulus drawing one gazelle after another appears to be a visual response to movement, and this following response is consistent with the idea that juvenile imprinting on the mother's rump provides adult society with an important social adhesive.

The emphasis on visual communication in these gazelles seems to be correlated with the abandonment of scent-marking with the preorbital glands in territorial and sexual behaviour. Instead, a territorial male marks his area with combined dung and urine deposits. The white rump, incidentally, serves to advertise excretory postures which are emphatically ritualized;





stretching while urinating and squatting while dropping dung (on the same spot) suggest a low-level but conspicuous semaphore and other gazelles respond to these postures with interest or retreat. In contrast, dominance finds expression at the front end of the animal and displaying territorials bunch their necks and tilt their horns while slowly strutting broadside on to one another.

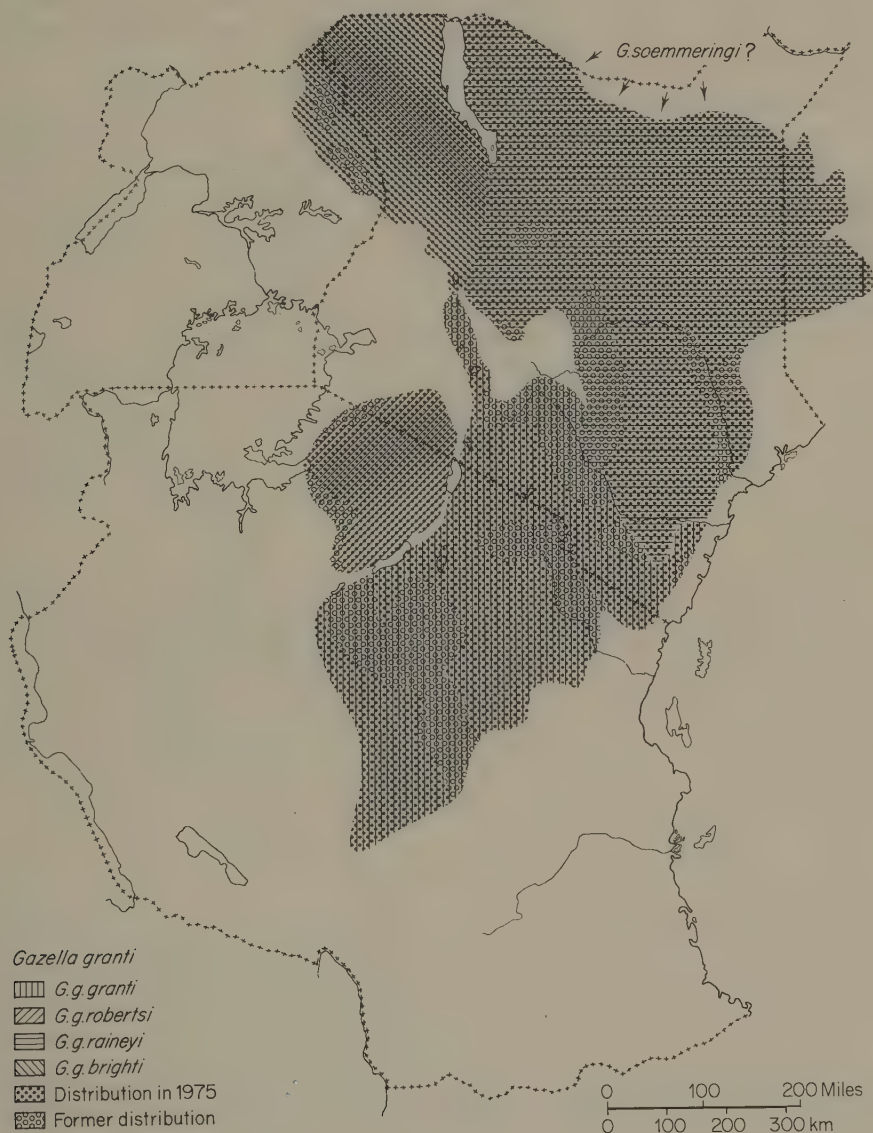
When present, the slanting stripes on the sides of the body might, from lateral viewpoints, serve as pointers or "indexic" markings to tail and white rump (Hailman, 1977). Their presence in some races and individuals and absence in others suggests that they are a vestigial pattern element. They are not twitched like those of *G. thomsoni*.

The range of *G. granti* encompasses all the drier parts of East Africa and extends north into the Sudan, Ethiopia and a small part of Somalia. Their habitat includes scrubby semi-desert, open savannas and treeless plains. They range up to 2,000 m in altitude. They prefer higher, well-drained areas during the rains but will move out on to flat, grassy valleys in the dry season. Wherever possible they avoid tall grass though small groups and lactating females can sometimes be found in acacia thicket country so long as it is broken up and is well traversed by paths and open swathes.



 *Gazella granti*
 *Gazella soemmerringi*

Grant's gazelle has been described as a seasonally adapted intermediate feeder preferring herbs and shrub foliage (Hofmann, 1973). During the early rains (and for a longer period on short grass plains) these gazelles include grasses in their diet; principally short species such as *Cynodon* and *Harpachne schimperi* but also the fresh shoots of species that are avoided at a later stage in their growth such as *Hyparrhenia* and *Themeda*. Once the grasses are longer and also during the dry season, *G. granti* mainly browse



from shrubs and short herbs. *Solanum*, *Indigofera*, *Sida* and *Disperma* have been recorded as common foods. Fruits of *Balanites*, *Solanum* and *Calotropis* have also been recorded in their diet. Hofmann (1973) illustrated the unusually large size of the salivary glands, which may be adapted to circulating fluid to cope with a relatively dry diet. He also noted that the stomach has more features typical of a concentrate selector than a grass eater. That

Grant's gazelle may benefit from overgrazing by domestic stock was pointed out in South Kenya, Talbot (1962) and he drew attention to some of the preferred foods being those which invade or become dominant in abused ranges. He found a ratio of about 40% grass to 60% dicotyledons.

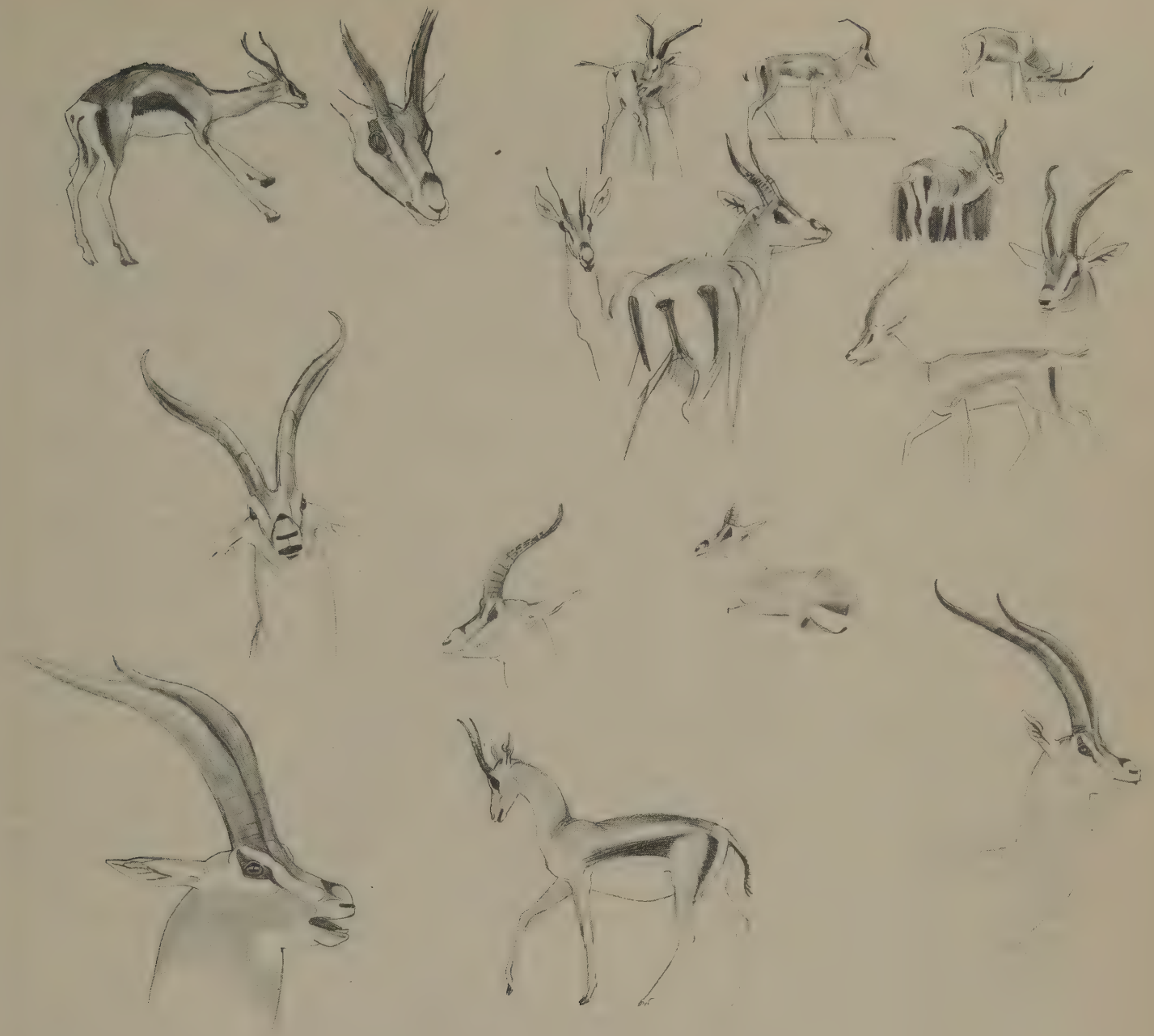
The density and overall range occupied by Grant's gazelles can be greatly influenced by the prevalence of herbs. In 1967 there were estimated to be 30,000 of these gazelles in the Serengeti National Park, in 1978 the estimate was 52,000. Sinclair and Norton-Griffiths (1979) attributed this growth in numbers to an increase in herbs following expansion of the gnu population. The grazing reduced competition from grasses which benefited the herbs and increased the gazelles' food supply.

Grant's gazelle are migratory, or at least make distinct seasonal movements over a large part of their range, but are resident in localities where there is adequate food around the year. The social system is well adapted to take advantage of a scattered and changing food supply by being exceptionally fluid. There are the usual groupings by sex, all-male bachelor parties, solitary territorials, mothers that become solitary while their new fawns are hidden, mother-young pairs or groups (which average between six and sixteen depending on the habitat). In spite of their unstable membership and migratory habits, Walther (1972b) discovered that female and bachelor groups quickly establish home ranges and repetitive daily circuits and that the two classes commonly mix and part in the course of a single day. Walther followed the movements of a mixed herd over 24 hours and found they had walked a circuit of at least 16 km within an area of about 20 sq. km.

Within their home range, females or female groups are detained by solitary adult males in their mating territories. Here mixed groups and other males are often tolerated but only the territorial males mate within this area. Walther (1972a, b) has described relatively large mixed herds arriving in Togoro as soon as the short rains fall. These tend to split up into male and female groups and some of the mature males acquire mating territories. At the peak of mating activity, other males may only visit established territories so long as they remain subordinate.

Walther stressed that annual cycles are greatly influenced by variations in local rainfall but his observations in Togoro, Serengeti during 1965 and 1966 suggested that there were two birth peaks, one in January, the other in August. The latter coincided with a mating peak and very numerous small female groups. As the dry season advanced, there was a general drift off depleted range. With the first rains very large mixed groups congregated on flushes of new growth and in December there was a wave of movement back on to the green plains. This was followed by the formation of territories and numerous small female groups which became progressively larger, reaching a peak in about May, when the gazelles are restricted by the growth of tall grass. With the onset of the dry season, these large groups fragment and the annual cycle is repeated.

In the Ngorongoro crater, Estes (1967) found resident female or nursery herds averaged 16.4 in number and bachelor groups 10.3. Large aggregations of several hundred animals may form on good grazing grounds but these break up very readily. Territories vary from a few hundred metres across



to several kilometres. Female groups are more likely to find adequate fodder within large territories and Walther (1968) noticed females sticking to a restricted area for relatively long periods but he had the impression that this was only possible under favourable conditions. Resident populations such as those in Ngorongoro have much smaller territories (8 ha). The temporary territories of migrant populations are less vigorously policed and are often without contiguous boundaries and in Serengeti territorial males can be one or more kilometres apart. Walther (1968, 1972) has described bachelors as having an hierarchical order of precedence, the younger less dominant males ahead and the other males in a group at the back or centre of the line. In challenges there is a distinct tendency towards equal matching of the opponents. Walther (1968) compared his observations of fights and challenge displays and the result suggested that fighting is progressively displaced by ritualized displays as the males mature.



A sequence of events commonly seen in the field has been described in detail by Walther (1965, 1968, 1972a, b, 1974) and Estes (1967). Two males approach one another with their heads slightly tilted away from one another; when they are about to pass one another, 5–10 m apart, they stop and, as if on a signal, whip their heads round to face one another, meanwhile throwing their heads back and up so that the neck bulges prominently. The head is also tilted inwards so that the span of the horns can be seen by the opponent and the outspread ears increase the pattern and visual impact of the head. Both males may then stand in this position, quietly returning their heads to a normal position, then flicking them back. The sequence may be broken off quite soon, may be repeated many times or they may keep moving in a circle. If at any stage one of the two neglects to present the side view of his body, or while head flagging happens to touch horn tips, this triggers an immediate horn clash. Where neither male is intimidated there are further preliminaries to actual fighting, including grooming movements, and repeated scratching of the neck and forehead with a hind-foot. Pseudo-grazing, thrashing of the horns in the grass and pawing are followed by the excretion ritual. If there is still no retreat, the males then confront one another and after a feint or two clash their horns. Once engaged they persist in pushing one another with their heads almost flat on the ground and sudden sideways twists may throw an opponent off balance. Estes has described this display as an exhibition of neck development and he has emphasized how experience of fights with other males might make this exhibition the more effective.

When females are in oestrus their condition is detected in the urine and the raised tails advertise sexual receptiveness. The male courts with a stiff prancing walk with head tossed or held high in the air while the tail is held horizontal. Copulation is sometimes achieved while the female is moving and the male is walking erect on his hind legs.

Gestation is approximately six months and the young are born in long grass.

“During parturition the female carefully examines the ground each time she changes position and ingests all fluids and membranes. The fawn is cleaned with equal thoroughness. Once it has gained its feet and sucked, the fawn seeks a suitable hiding place, watched by the mother, who evidently memorises its position by observation from several vantage points before moving away and beginning to graze.” (Estes 1967)

Whereas births in northern Tanzania are in January, February and August, Karamoja births, north of the equator, have been recorded in June and November–December.

All the major predators kill Grant's gazelle but cheetah, wild dogs and, in some localities, jackals are undoubtedly the more important. In northern Karamoja they have been observed to be particularly vulnerable during the rains on soft ground and in this area the cheetahs feed almost exclusively on Grant's gazelle at this time.

Walther has compared the flight distances of *G. granti* and *G. thomsoni* and found female Grant's were the shyest of all. This may be modified when there is a young one in the vicinity or the mother may actively attack

small predators. A female has been seen to chase a baboon for three hours after it had killed her fawn. Maloiy (1963) has summarized the effects in Kenya of ranching, settlement, shooting and fencing on the gazelles and their habitat. As a conspicuous and easily killed species with good meat and a valuable skin, *G. granti* will need to be adequately protected if they are to survive and realize their potential as a useful source of protein on semi-arid or sub-desert ranges.

In Karamoja, Grant's gazelle is one of the tribe's four major totems and is highly regarded as a creature of outstanding beauty.





**Soemmering's
Gazelle
(*Gazella
soemmeringii*)**

Family

Bovidae

Order

Artiodactyla

Local names

Holli dahan (Afrendille), Aoul (Somali).

Measurements

head and body

135 (125—150) cm

height

85 (81—90) cm

tail

20 (18—23) cm

weight

40 (38—46) kg

horns

30—52 cm

Soemmering's Gazelle (*Gazella soemmeringii*)

Races

Gazella soemmeringii butteri

Sommering's gazelle is reported to occur sporadically from the Chalbi desert in Rendille country eastwards to Gallaland (Sato, personal communication).

This species and Grant's gazelle resemble one another so closely that they may be readily confused and the situation in the region of overlap and along the margins of the two species' ranges requires careful investigation if a realistic definition of the two species' ecological roles are to be achieved.

The two species are broadly allopatric but the southernmost race of Sommering's, *G. s. butteri*, apparently comes into contact with the northernmost race of Grant's gazelle, *Gazelle granti*, in southern Ethiopia and northern Kenya. Curiously *G. s. butteri* has more superficial resemblance with *G. granti* than the larger northern races in that it has faint pygal and flank stripes.

The principal distinguishing characteristics are more extensive white on the rump, strongly marked facial blazes, a large head and heavy but short backward-sweeping horns that have a lyrate shape with in-pointed hooked tips. They are long in the leg with big hooves and the relatively short neck may be correlated with the somewhat elongated head. It is probably in overall body proportions, with the alteration in mien and gait that go with them, that the two species can best be told apart.

Belonging to the subgroup "Nanger" this species is related to both *G. dama* and *G. granti*. Overall distribution of the three species is allopatric and Lange (1971) has drawn attention to an ecological gradient, *G. dama* inhabiting the driest extreme and *G. granti* (which he regards as the most evolved species) preferring the flatter, more open but generally moister habitats of sub-arid East Africa. This gradient also applies to relative population densities and these may have a meaningful correlation with the length and complexity of shape of the horns.

G. soemmeringii occupies a more pivotal position, being restricted to the Horn of Africa and with a distinct preference for rough, hilly country with scattered evergreen thickets and wooded steppe dominated by *Acacia* and *Commiphora* species although it occurs on grassy plains.

Like *G. granti* this species is reported to both browse and graze but its habitat preference suggests that grass plays less of a part than it does in the diet of *G. granti*. Some dominant potential food plants in its habitat are *Sericomopsis*, *Blepharis*, *Indigofera* and *Tephrosia* and, of course the major tree species *Acacia* and *Commiphora*. The most widespread and dominant grass in this region is the palatable *Chrysopogon aucheri*. They are able to survive without drinking water.

Formerly the most abundant and widespread of gazelles in the Ogaden,



Eritrea and much of Somalia, Bolton (1973a) and others have reported a very substantial decline throughout its range in Ethiopia and Somalia. Hunting has probably contributed to this decline but intensive stockraising may be the primary reason. They have been seen associating with oryx, hartebeest and domestic camels. Only at high densities could the latter be an important competitor, but overgrazing and overbrowsing by cattle, sheep and goats would certainly prejudice their survival. Seasonal movements have been recorded for this species, as they have for *G. granti* and *G. dama*. In the Kassala region of the Sudan they move out into the desert with the arrival of the rains and return southwards to the valleys and foothills before the drought sets in.

It is perhaps during these movements that congregations of a hundred or more animals have been recorded. The more usual pattern is of mixed, but predominantly female groups numbering about six or seven, and solitary males of all adult age classes.

The species is apparently territorial but the preorbital glands, which are not very highly developed, have not been seen to be employed for marking, at least not in captivity (Walther, 1968). Walther remarked on the unusual frequency with which the males of this species scrape the ground with the boss of the horns during territorial encounters or fights and he described them making a sideways link during fights, a tactic that must be assisted by the strongly hooked inward curl of the horn. Earth scraping is certainly easier for a gazelle with backwardly swept horns than it is for species with more vertical ones, and it is significant that wear shows more on the forward surface of the horn bosses of aged male *G. soemmerringii* skulls whereas it is the tips of the horns that wear in *G. thomsoni*.

The dung and urine ceremony is as pronounced in this species as in other gazelles (Walther, 1968) but a female in Hanover Zoo often deposited her dung on top of that of the male. The erect proud posture of territorial male *G. granti* and *G. thomsoni* when they approach a female is, according to Walther, less characteristic of *G. soemmerringii*. During the initial stages of courtship the male resembles some non-gazelline antelopes in approaching the female with the head stretched forward in a lowered position.

The run or gallop is said to be fast, interspersed with high long bounds and it is possible that its limb proportions are influenced by adaptation to relatively rough terrain. Disparaging terms have been used by hunters comparing the gallop of this species with the "graceful" gait of the plains' gazelles.

Births are said to occur at the peak of the main rains, in April, in Somalia. This would ensure ideal grazing conditions, moisture and cover, for both mother and offspring. Assuming a gestation of six or seven months, the mating season would therefore take place during the light rains in about October.

Walther (1968) noted several peculiarities in the courtship rituals of this species in captivity. Instead of the usual *laufschiag*, a vigorous kicking out with foreleg, there was an emphatic one-two-three step march with stiff forelegs, which instead of inducing the female to stand still provoked flight. Thus the pair proceeded by fits and starts in a wide circle or arc. The female walked with sharply erect head and neck with the ears back; her rump tended

to be lowered and her tail waggled incessantly, copulation was achieved while both animals were on the move, the male walking on two legs; a remarkable feat in accuracy of aim and timing.

The remoteness of the borderlands from which this gazelle has been reported may explain why the species has not been previously recorded in Kenya. Seasonal movements carrying the animals across frontiers may also mean that they are not permanently resident but there is obviously a need for further information on this declining species.

Soemmering's gazelle has a special interest in that it has become isolated on Kebir island in the Dahlak archipelago, where it has developed a dwarf form. Information on the anatomical, physiological, ecological and behavioural implications of size could be gathered by comparing the dwarf form with the much larger race, *G. s. berberana*, which occurs on the Haud.



Gerenuk
(*Litocranius*
***walleri*)**

Family

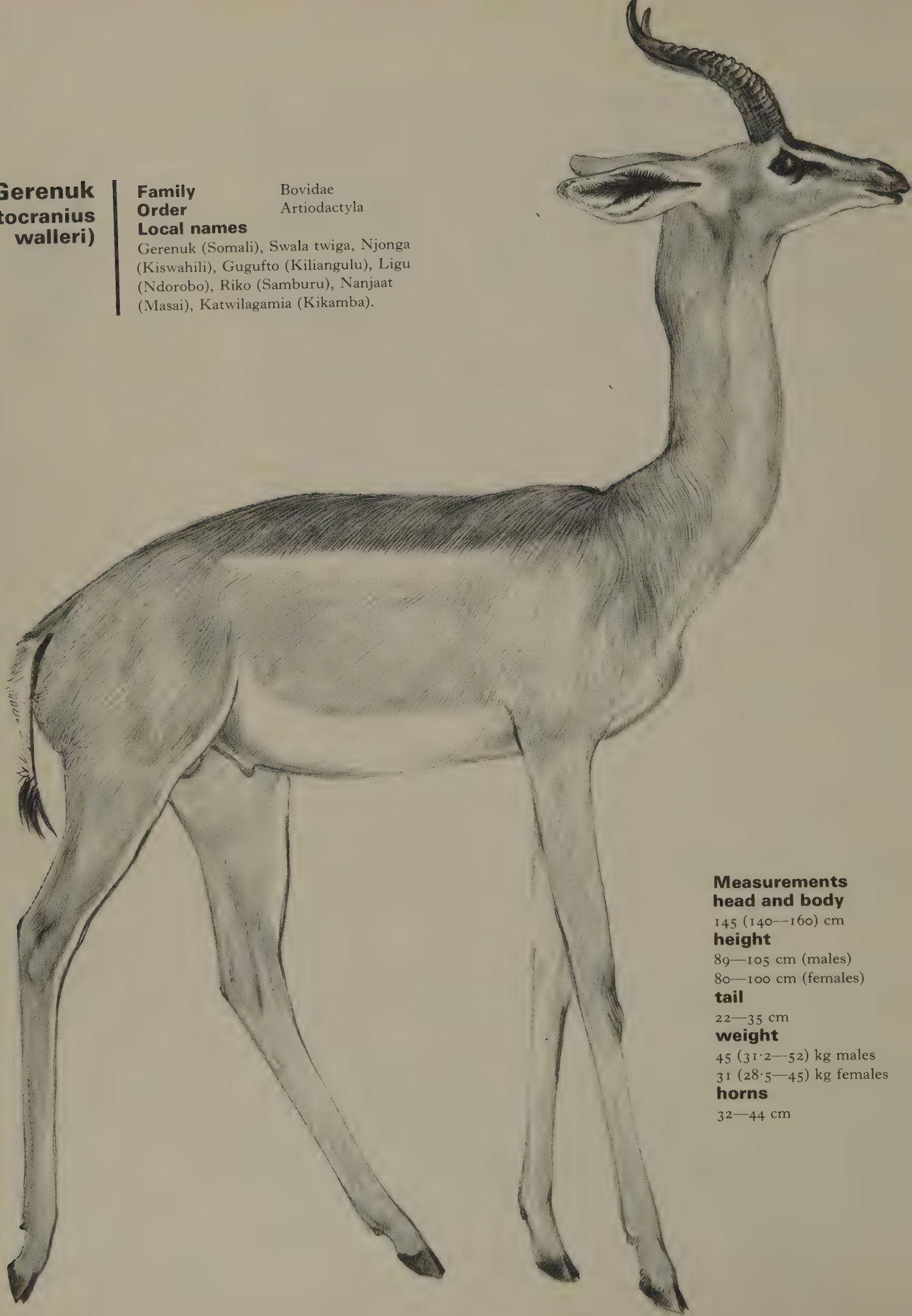
Bovidae

Order

Artiodactyla

Local names

Gerenuk (Somali), Swala twiga, Njonga
(Kiswahili), Gugufto (Kiliangulu), Ligu
(Ndorobo), Riko (Samburu), Nanjaat
(Masai), Katwilagamia (Kikamba).



Measurements
head and body

145 (140—160) cm

height

89—105 cm (males)

80—100 cm (females)

tail

22—35 cm

weight

45 (31.2—52) kg males

31 (28.5—45) kg females

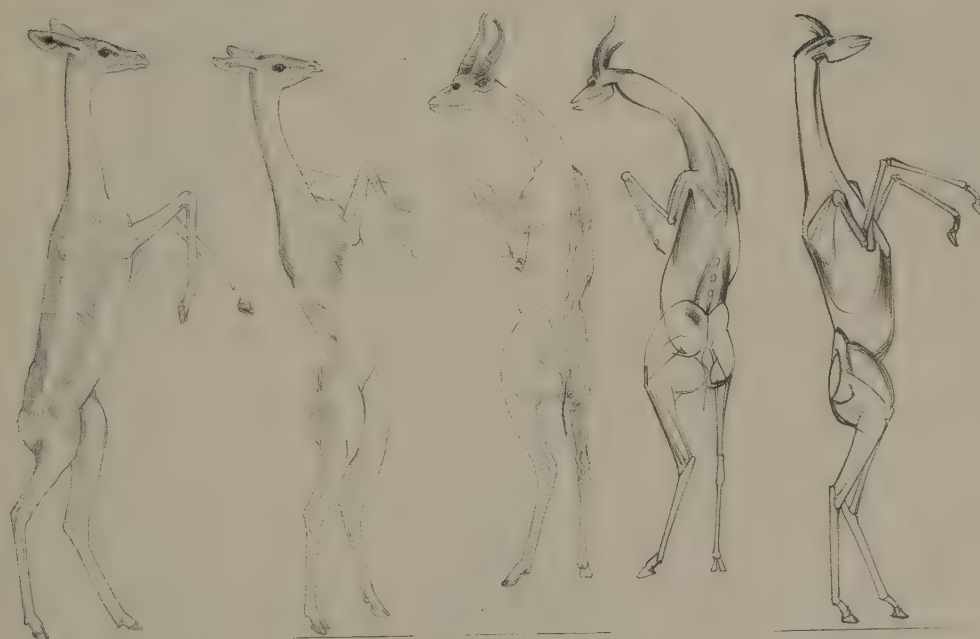
horns

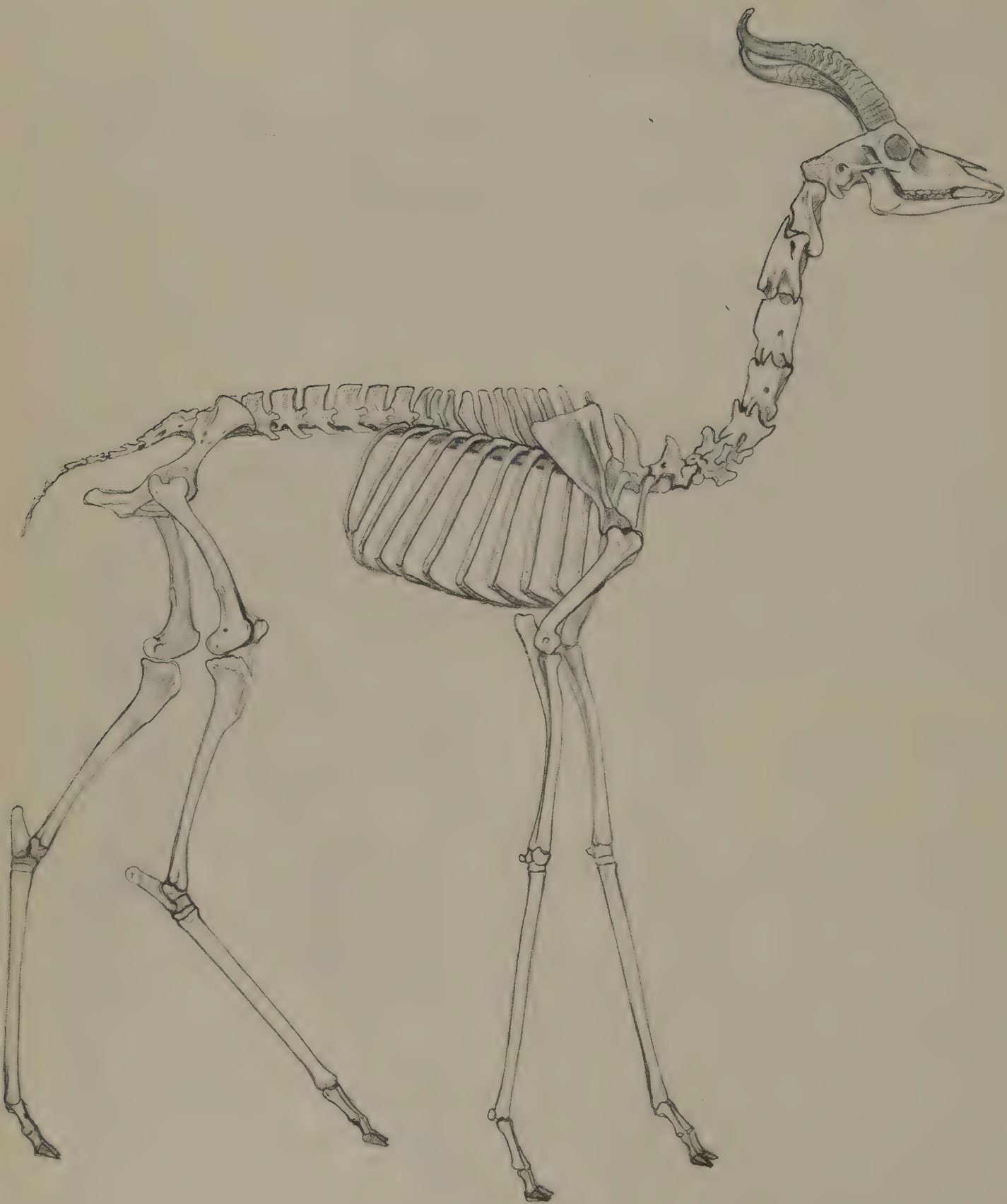
32—44 cm

Gerenuk (*Litocranius walleri*)

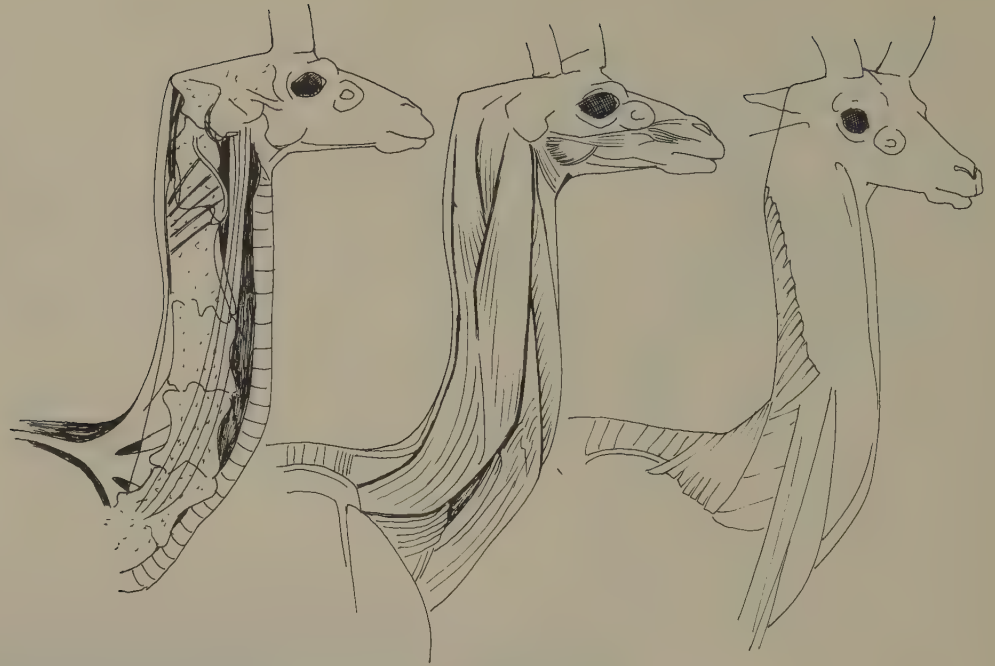
When a species departs from all its nearest relatives in shape and proportions the differences usually signify some peculiar specialization. In the case of the gerenuk, its odd proportions derive from the strategy it has adopted to get its food in a difficult environment rather than the actual diet, and its behaviour resembles that of many other antelopes in its overall pattern.

The gerenuk's diet and mouth parts are not greatly dissimilar to those of some pigmy antelopes in that the animals browse leaf by leaf and shoot by shoot off the green foliage of trees and shrubs. This piecemeal and relatively soft diet does not demand much chewing and the molar tooth row is only 5 cm long and is mounted in exceptionally shallow mandibles. The elongation of the maxilla into a pointed but diminutive muzzle adds to the impression of shallowness. This very small mouth belongs to a surprisingly large animal but the disproportion is partly due to the length of the legs and neck. The long limbs are not adapted for speed but are essentially a means of increasing the animal's reach, an extension that is augmented by the habit of standing on two legs. The animal can not only rear up on its hindlegs but can also maintain its balance in the bipedal position without supporting its forelegs. The anatomical implications of this posture have been investigated by Richter (1970), who noted the exceptional strength of the metacarpals and modification of the lumbar vertebral spines to accommodate a marked lordosis in the small of the back when the animal stands upright (see drawing).









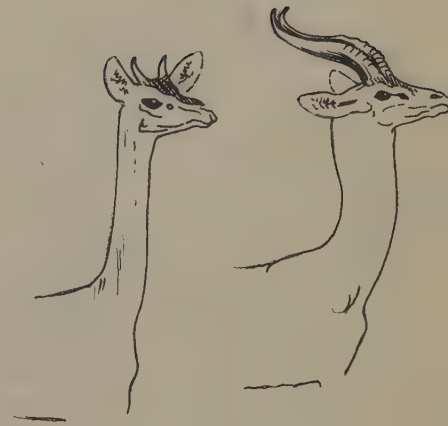
Sketches showing principal muscles operating head movements in gerenuk.

The slender neck is caused not only by a lengthening of the vertebrae but by the fact that several of the superficial muscles that would link the shoulders with the head in other ungulates are of reduced importance in the gerenuk and have retreated down the neck (notably the splenius, brachiocephalicus and sterno-mandibularis). The extra length of the neck has increased the gerenuk's access to shoots and leaves, but the reduction in bulk counteracts a trend that is very pronounced in the male of most antelope species in which a robust and muscular neck transfers power from the limbs and the weight of the body up to the butting, ramming head and conversely absorbs and transfers the pressures and shocks coming from the rival's weight or blows. The slender neck and legs of the gerenuk are totally unsuited to withstand the force of body weight in a head-on collision so this species has developed a unique form of fighting in which the heavy horns



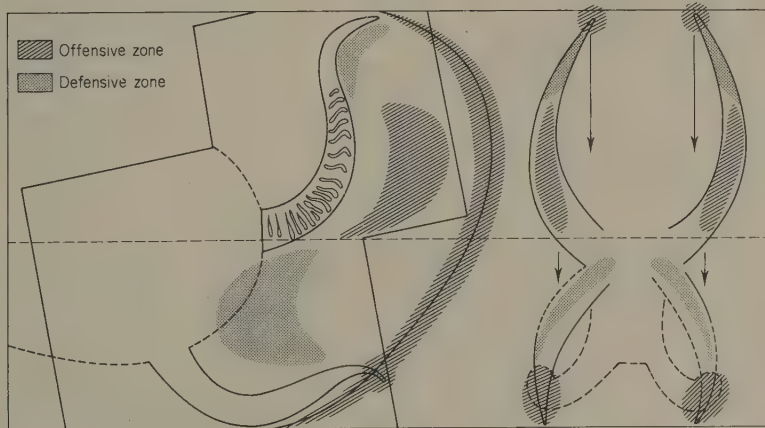
are clashed together by means of violent nods of the head. Conducted with the head down near ground level, this mode of horn clashing has the advantage of keeping the delicate muzzle and jaws shielded while the lyre shape of the horns, with strong terminal hooks, is well designed to catch and parry blows. Should a horn happen to strike through the defences, it encounters thick nape skin and still thicker bone.

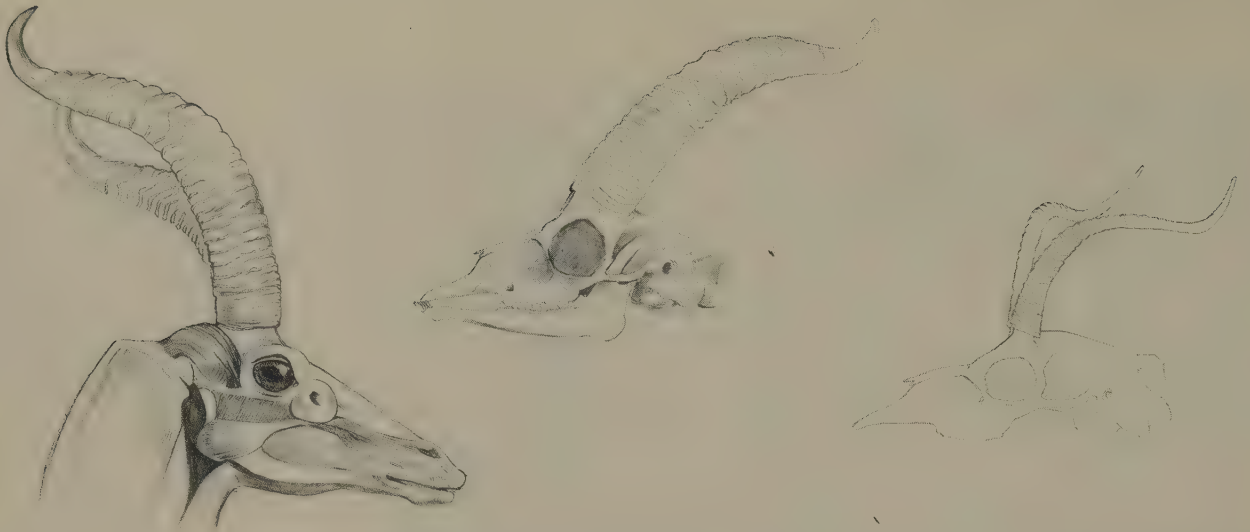
The thickening of the cranium not only protects the brain from blows but also provides very necessary buttressing for the phenomenally heavy horns. Furthermore there must have been intense selection in this species for both weight of horns and maximum local leverage at the base of the cranium. Because a high proportion of the powering of the horn clashes derives from the muscles of the upper neck, the leverage of a blow must increase with the distance between the horn base and the articulation at the occipital joint. It is this need for added leverage that explains the backward extension of the cranium in this species and the massive reinforcement of this bony cantilever is also very necessary to withstand the stresses of clashes. Opposite forces can be exerted on the horn depending on whether impact is on the back of the hook in an upstroke or on the forward ridge in a downstroke. The principal muscles powering the downstroke are the *longissimus capitis* and *longus capitis* while the opposite movement is operated by the *semispinalis capitis* and *rectus capitis*. The purchasing surfaces for these muscles on the nuchal vertebrae and on the occiput and mastoid process are appropriately large and the muscles are so big in an adult male that the neck is noticeably thicker at the upper end than it is near the base. The deeper muscles of the upper neck possibly achieve greater independence of action through the retreat of the long superficial muscles which normally assist the movement of the head, but these muscles have also declined in other long-necked animals such as the camel and the giraffe, which do not put a premium on independent nodding of the head.



Right: diagram of leverage and reinforcement in skull and horns.

Below: Diagram of the arcs of movement and zones of offence and defence in gerenuk horns, as seen from lateral and frontal viewpoints.





Dissection showing small size of masseter, a normal skull and one with exceptionally slender horns (sex unknown).

Neither the elongation of the cranium nor the nodding action are restricted to the male gerenuk. From an early age both sexes commonly nod and rub their heads together. Even adult females tend to nod quite vigorously in various contacts with other females and with their young. It is possible that head-knocking might serve as a greeting ceremony by allowing females to establish some sort of dominance order, no matter how temporary but the existence of this specific trait raises the interesting possibility that the females have also ritualized an action pattern that evolved in the context of competition between males.

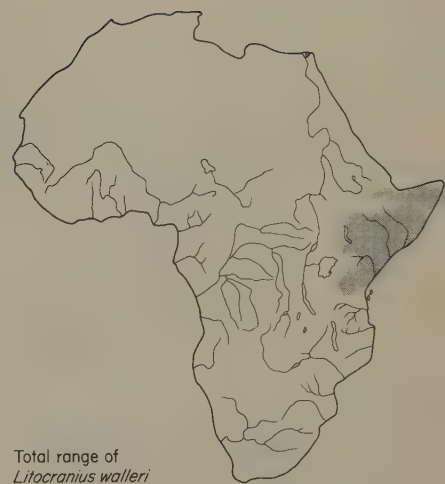


The colouring of the gerenuk is so remarkably similar to that of the impala that it must raise the question of what the special advantage of a three-tone russet coat can be. Certainly the white belly becomes very conspicuous indeed when animals are browsing in the upright position.

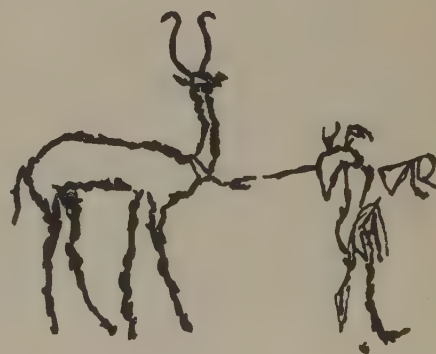
The gerenuk is endemic to the semi-arid areas of North-East Africa. There may have been extensions of range during arid periods of the late Pleistocene but it is interesting that they do not exist in South-West Africa, where conditions are not dissimilar to those in the Horn of Africa.



The gerenuk is beautifully represented in ancient Egyptian tomb paintings of the New Kingdom as tribute to the Pharaoh Rameses II. There is also evidence that the gerenuk once ranged all along the wedge of land between the Red Sea and the Nile. Near Aswan there is a rock engraving of about 3—4,000 B.C. depicting a male gerenuk being led by a man on a string (see drawing opposite) (Winckler, 1939).



Stone engraving from Wadi Sab' er Rigel, east of the Lower Nile 4,000—9,000 B.C. (after Schomber, 1966).

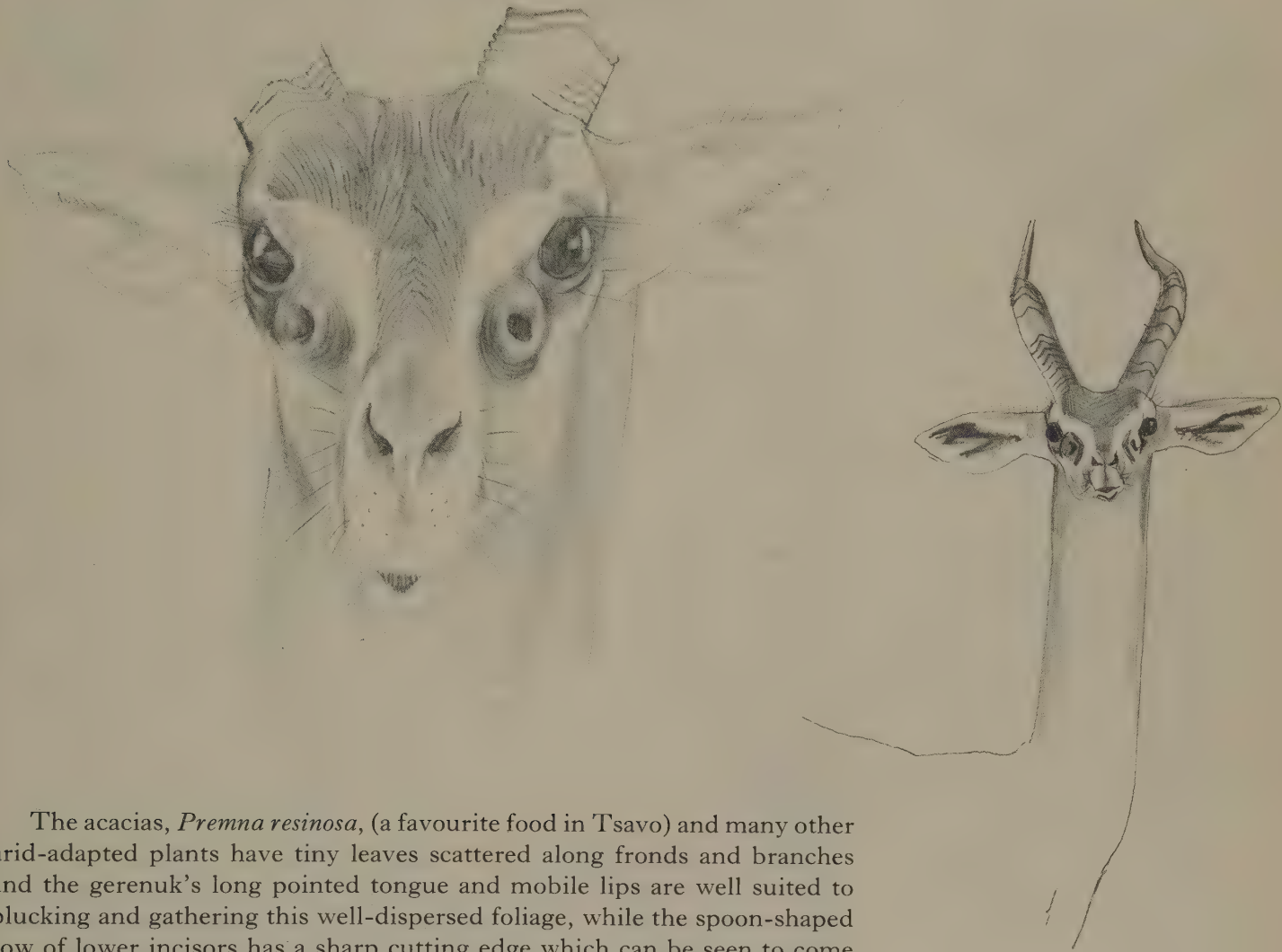




Dependent on an abundance of bushes and small trees, they nonetheless avoid true thickets and are commonest on flats where *Acacia*, *Commiphora* and other dry bushland species are well spaced apart as individual plants or are grouped in small clumps.

The abundance of gerenuks in such habitats is probably due to their having access to a higher proportion of the available browse; for the animals stay on the periphery of bushes and they do not put themselves in positions where they might find disengagement difficult. Their long necks allow them to browse over the canopy of low flat-topped bushes, while a bipedal stance may allow them to reach up to 2 m into the expanding upper portion of *Commiphora*, *Acacia* and other fan-shaped bushes. They do not normally browse at ground level and they never eat grass.

They feed skilfully on the thorny species that are numerous in this habitat. The diet is very catholic and although Leuthold (1970a) found some common species, including succulents, were rejected altogether he recorded them eating 68 species of plants. Some of the dominant species provide them with the bulk of their food but seasonal and regional variations in diet may be determined very largely by what plants are in bud or leaf at the time and whether they are within reach. The choice of food is greatly increased during the rains, at which time dry-season staples, such as *Boscia* may be ignored or eaten less frequently.



The acacias, *Premna resinosa*, (a favourite food in Tsavo) and many other arid-adapted plants have tiny leaves scattered along fronds and branches and the gerenuk's long pointed tongue and mobile lips are well suited to plucking and gathering this well-dispersed foliage, while the spoon-shaped row of lower incisors has a sharp cutting edge which can be seen to come into play when the animal plucks foliage with small upward nods. The small muzzle can reach through the barricade of thorns that often protects foliage, while vibrissae and eyelashes are well placed to anticipate any danger to the eyes. The ears are also covered in a stubble of short hairs that may have a similar function. The small mouth may also influence the gerenuk's preference for the fresh shoots of some of the large-leafed plants such as *Combretum*, *Cordia* and *Ehretia*.



Left: alert but submissive or fearful subadult. Note high angle, thin neck, ears up and back.

Right: alert dominant adult male with thick neck, ears out and forward.

Below: carpal brush.



Gerenuk do not drink. They are most active at dawn and dusk and also browse at night and in the early morning before dawn. From about 9 a.m. to 5 p.m. they stand or lie in the shade or shelter in thin cover. When forced to run, they go at a long lope with the head held low, but they are not particularly fast in spite of their long legs.

The females and young sometimes lie flat on the ground in response to a disturbance; they also tend to cluster close together. Males, instead, may display more curiosity and I have noticed that the ears of confident mature males make a highly characteristic configuration with the horns and thick neck, which contrasts very strongly with the slender silhouette of females or subadult males, which tend to carry their ears in a retracted position when hesitant.

Adult males are highly territorial and Rainey (personal communication) has found that boundary areas between territories are detectable from a high frequency of orbital gland deposits; dung appears not to be used for the demarkation of territory. Leuthold (1971a) found no evidence of any overlap in the home range of adult males. He found that they are generally very conservative about their home range, which covers areas of 3–6 sq. km in Tsavo; however, he did find one female that shifted its range. The tendency for individuals to stick to a small locality may give a false impression of group stability, for Leuthold found that the only consistent association was that of a mother and her offspring.

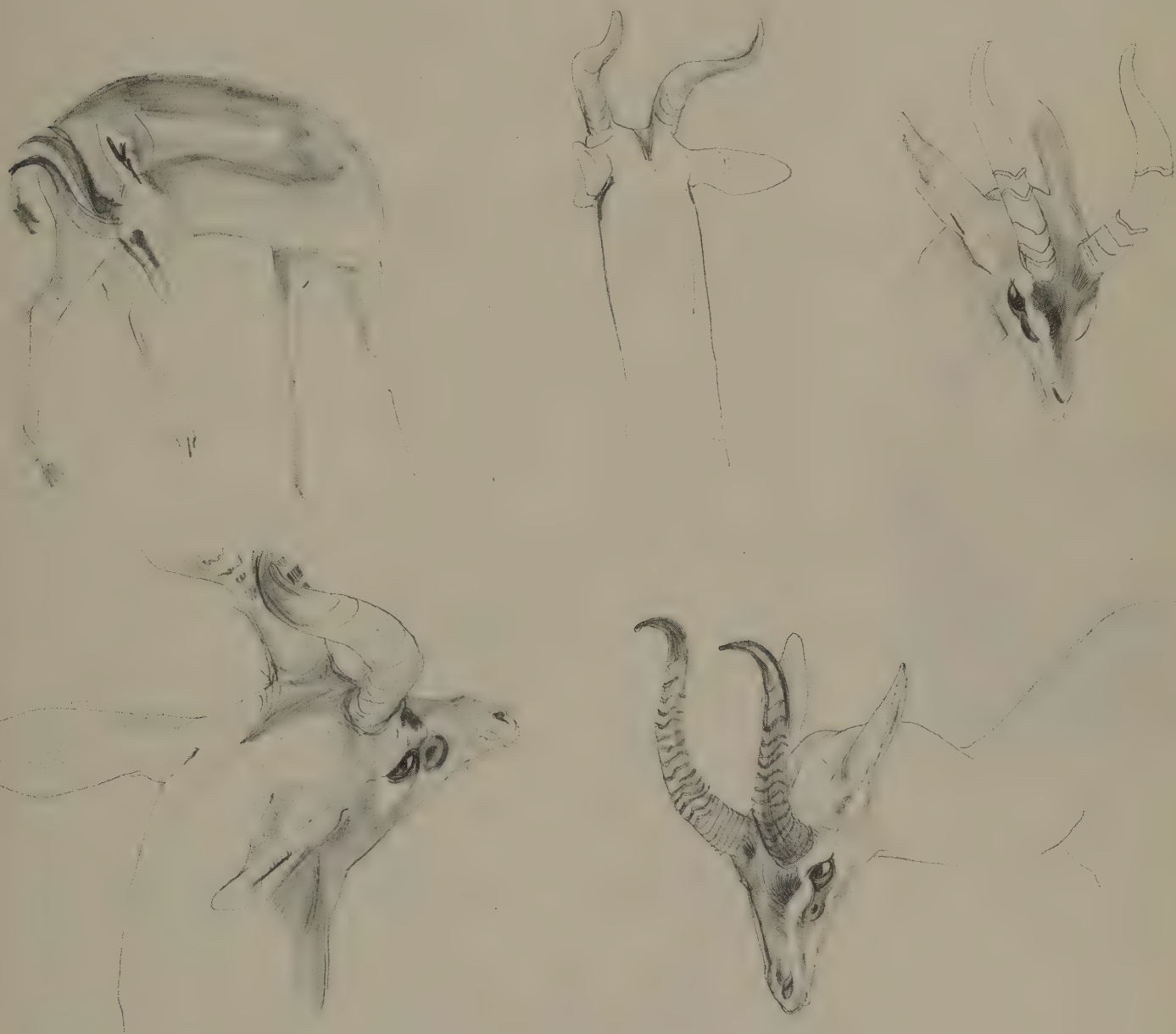
Groups of two to ten are not uncommon and Schomber (1966) recorded up to 30 gathered together in what was probably a casual and ephemeral association. Densities must vary greatly with the habitat and while those in Tsavo may reach optimal numbers in some localities the overall average for this Park is low and has been estimated at only 0.39 per sq. km (Cobb, 1976).

There is never more than one fully adult male in one party but subadult bachelors (generally in a very scattered formation) may form groups numbering up to nine individuals. Females accompanied by one or two offspring may be herded together by a territorial male and Leuthold described males seeking to annex females when “sexually motivated”. Ullrich (in Gzimek, 1972) reported that the male’s upper neck was capable of thickening and suggested that this might occur during a mating season but no detailed observations on the periodicity of the gerenuk’s reproductive or social behaviour have been published and Ullrich may have seen the maturation of young males.

The adult male not only uses its orbital glands on twigs (that may have had their leaves stripped off previously) but it also rubs them on the hind-quarters and shoulders of females. Leuthold (1971a) has described males threatening females with a short rush and lowered horns and making a rumbling noise but, apart from a buzz of alarm, they are rather silent animals.

Females and subadult males signify submission by running or turning with tail raised or they may lie down stretched out on the ground, from which position the male may rouse them with gentle prods of the foreleg. The same gesture is incorporated in courtship as a slow *laufs Schlag* beneath the female’s belly. The male stands very erect when copulating.

Young are mostly born during the rains but they are well hidden and only accompany the mother when fully active. More than one generation of offspring may accompany the mother.



Alcelaphines

Alcelaphini

Genera

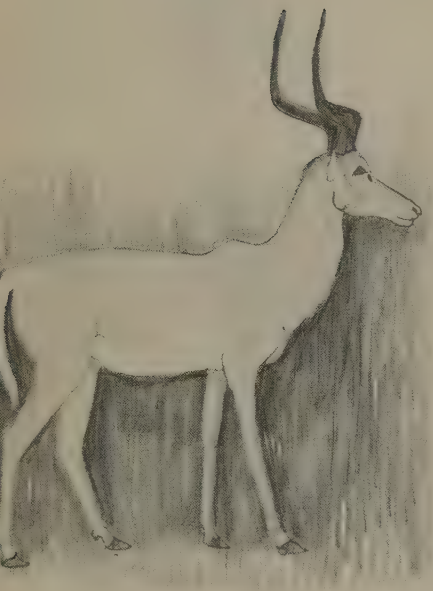
Alcelaphus

Damaliscus

Beatragus

Connochaetes

Aepyceros



Hirola, *Beatragus*.

Several mammalian lineages are best adapted to function within a very limited range of body size. When larger forms evolve out of such lineages it is not unusual for extensive remodelling to occur. Thus the common origins of hyaenas and mongooses are difficult to discern in the living animals; porcupines scarcely seem to be rodents and affinities with horses are lost in the unique mass of a rhinoceros.

Likewise it is not immediately obvious that increasing body size in gazelle-like antelopes should give rise to the peculiar proportions of the Alcelaphini. However, on closer inspection very many of the latter's features can be seen to manifest antilopine origins.

To begin with there is a common adaptation to running. The most important indication of the effects of greater weight without loss of speed shows in the joints. Condylar surfaces have longer fore-aft articulation and ligamentous sheaths around the major joints are exceptionally strong and well-developed in all alcelaphines. The hartebeest, *Alcelaphus*, topi, *Damaliscus*, and Hirola, *Beatragus*, have kept the long legs, speedy gaits and alert demeanour typical of Antilopini. A more usual effect of increasing body weight on limbs is for them to get proportionately shorter and thicker. This trend is just perceptible in the gnus but, nonetheless, they remain capable of considerable speed. To maintain speed in a heavier body the leverage of the limbs requires that the distance of body from ground must also increase. Grazing and drinking require that the neck or head should elongate by the same ratio.

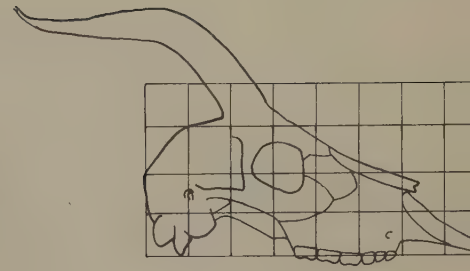
In the impala, (commonly classed with the Antilopini but treated here as a specialized offshoot of the earliest Alcelaphini, see p. 11), the social, hornless females remain within the weight range and retain the proportions of gazelles, notably the long neck and legs. The heavier, horned males also have long necks but have responded to the extra stresses of fighting by hyper-development of the neck muscles and by increasing curvature and length in the two inverted horn arches (so that blows can be delivered, caught or locked over longer surfaces) and by widening the span, thus broadening the horns' catchment area and dulling the impact of blows before it reaches the head.

Whereas the predominant stress on a gazelle horn is fore and aft, the impala's wrestling and jousting exerts lateral as well as frontal pressures; the horns therefore have circular rather than elliptical sections. For their

length the impala's horns are also lighter and more flexible than those of gazelles, being more horn and less bone and having hollow bases.

The horn cores of gazelles are dense, solid bone and their flattening is partly necessitated by a restricted anchorage above the orbit. These limitations have probably imposed evolutionary constraints upon the fighting methods and morphology of gazelle horns, whereas an early antidorcine–alcelaphine lineage may have overcome a structural obstacle to horn development because the skull developed sinuses in the frontal bone. The sinuses, which also extend into the bases of the horns, might increase the overall flexibility and lightness of horns but, more important, they effectively root the horns on to a greatly enlarged frontal plate, meanwhile insulating the cranial and orbital capsules from the impact of blows, no mean consideration for a large antelope.

I have pointed out in earlier volumes how surface plates of bone and cranial sinuses can allow gross remodelling of a skull with minimal distortion of the underlying functional units or separately encapsulated activities (Vol. I, pp. 94, 142; Vol. IIIB, pp. 10, 197).

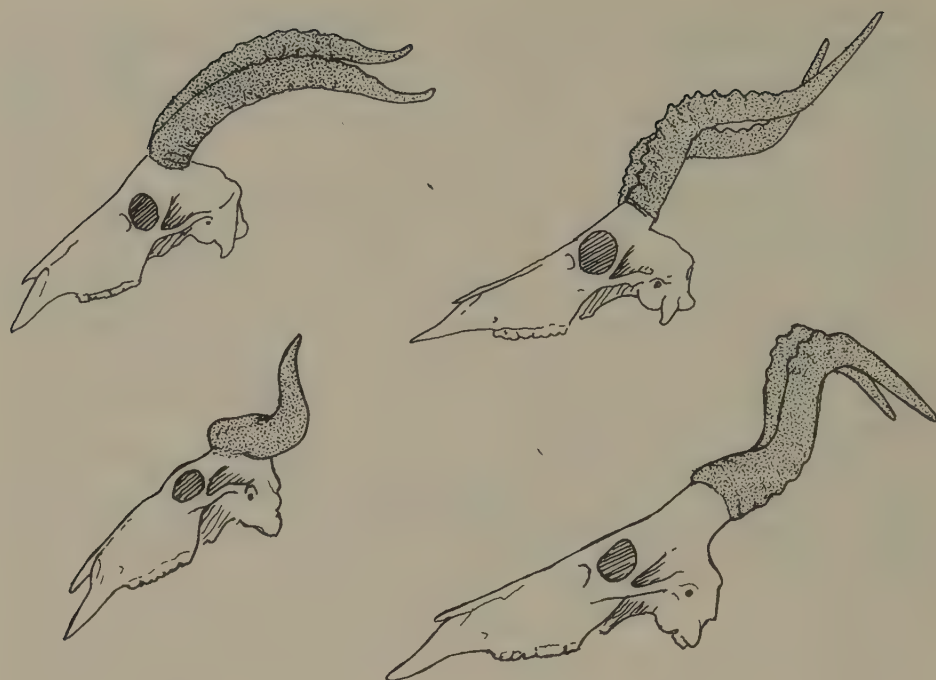


Above: reconstructed proto-alcelaphine.

Below: dissection of facial musculature in *Beatragus*.



Frontal sinuses are a diagnostic feature of the Alcelaphini and their prominent development in the skull of the impala lends support to the inclusion of this aberrant antelope in this bovid tribe. The horns of the impala and Hunter's hartebeest, *Beatragus hunteri*, exemplify one of four major trends in the Alcelaphini, each of which represents a different elaboration of and balance between the four functional horn activities, i.e. stabbing, catching, locking and ramming, the structural manifestations of which are spikes, convex arches, hooks and concave arches or bosses.

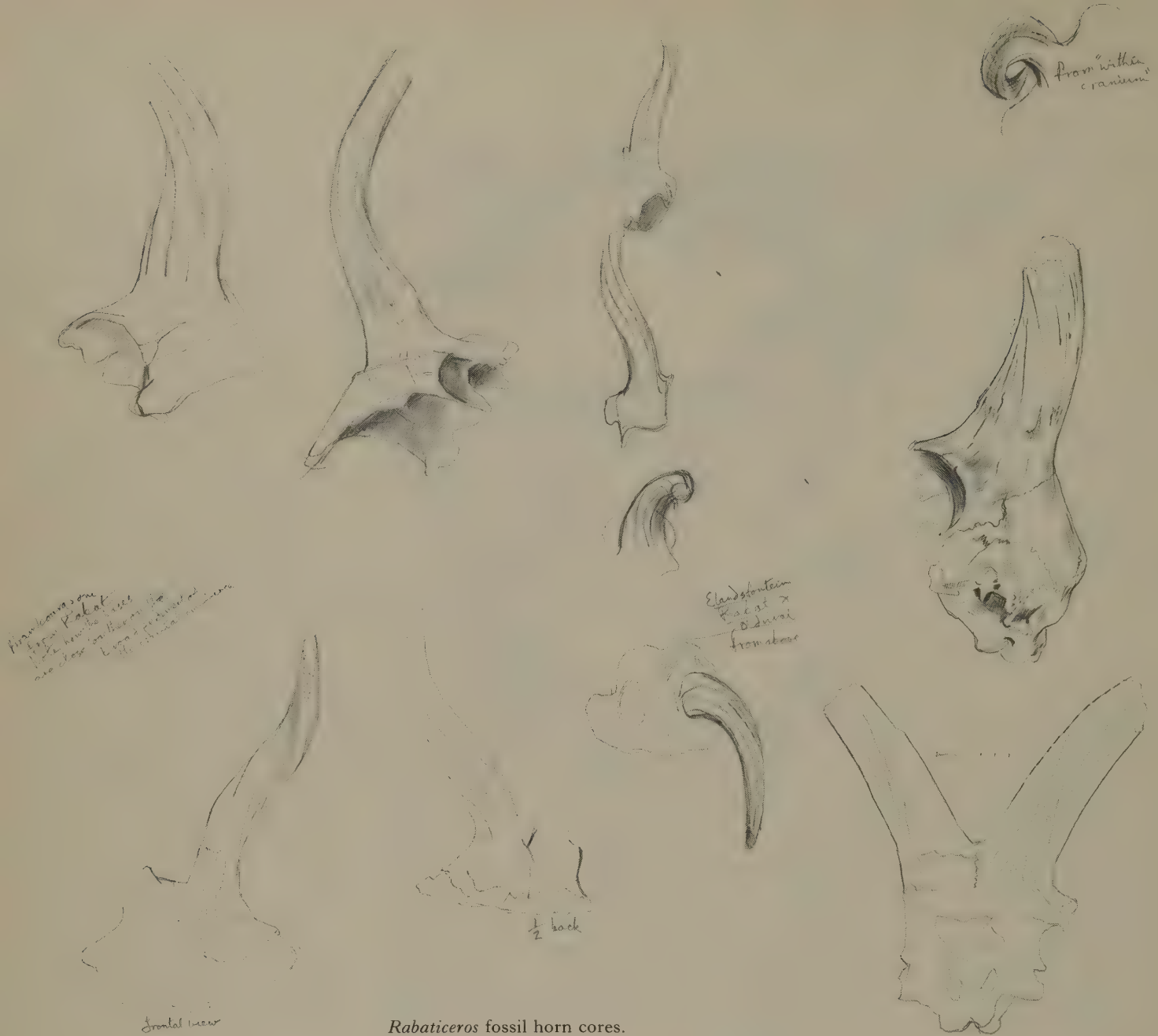


Skulls of top left: *Damaliscus lunatus*;
top right: *Beatragus*; bottom left:
Connochaetes; bottom right:
Alcelaphus.

The four structural types are: a) Simple enlargement of the gazelline type of horn (but with a circular section). Weakly convex and then concave and about 30—60 cm long, exemplified by the genus *Damaliscus*. Ramming or clashing is along the forward arch, catching and locking in the open “V” of the horns is loose and inefficient. b) Elongation of this double-bent type of horn with substantial increase in amplitude and curvature. Measuring 50—90 cm and exemplified by *Aepyceros* and *Beatragus*. This more highly differentiated horn has already been described and the four functional zones are clearly recognizable. *Beatragus* horns are very much thicker than those of *Aepyceros*, particularly in the stem and along the basal arch where the main force of a clash is expended. c) Lateral splaying of the horns, which enlarges the catching area but exposes the forehead, which must be protected therefore by the frontal sinuses and reinforcements of the horn base. This opening up of the crown to close-contact combat is usually associated with hooked horn tips for grappling. This horn form is typified by the gnus, which have evolved thick bosses on the forehead and sharply recurved the tips of their 40—65 cm horns. The extinct giant alcelaphine *Megalotragus* had splayed horns measuring a metre or more with an open span and undulating shape. d) Inflation of the frontal sinuses to cantilever the entire horn complex up and backwards, away from the face. This exceptional elongation and moulding of the frontal bones into a single stem or “handle” is matched by elongation in other bones of the face and constitutes the principal characteristic of the genus *Alcelaphus*. Hartebeests have some of the most complicated of horn shapes among bovids and they are manipulated while fighting like peculiar mechanical or surgical tools. They have spiked, looped, hooked and buffered surfaces and there are substantial differences in horn shape between the various allopatric races.

Opposite: hartebeest, *Alcelaphus*
buselaphus lichtensteini.





Rabaticeros fossil horn cores.

While each of the four structural types tends to emphasize particular components, some regional populations within a single lineage, such as *Alcelaphus* or *Damaliscus*, show variations in the orientation or curvature of horns, or remodelling of the frontal sinuses which alters their shape quite fundamentally. The original phyletic branching of the Alcelaphini must owe much to similar transformations in early ancestors and apparently intermediate forms of living species can usefully illustrate evolutionary trends, particularly when localized populations recapitulate some significant feature in the elaboration of horn shape.

For example, the Tsessebe, *Damaliscus lunatus lunatus*, differs from other damalisc races in an outward swivel of the horns from the forehead instead of a backward sweep. Not only does this anticipate laterally splayed horns of the gnu type, it illustrates the first step in the evolution of *Alcelaphus*-type horns.



Gentry (1978a) considered that *Alcelaphus* evolved within the last one million years via a fossil genus *Rabaticeros*, which derived from a damaliscine ancestor, *Parmularius*. The principal characteristic of *Rabaticeros* is a sharp twist (manifested in the surface grain of the bone) at the base of the horn core so that the double curvature of the damaliscine horn is simply back to front, turning the forward facing hook round to face backwards. Because the twist is mainly in the basal section the original "S" bend is retained intact but reversed.



In the horn of an adult *Alcelaphus* there is no hint of this phylogenetic history, because the grain, unlike that of *Rabaticeros*, follows the axis of the horn. However in an actively growing horn there is a narrow germinal band where skin meets horn and under it, at the back of the horn core, there are granulated filaments of bone typical of the interface between the core and its bony sheath. When a hartebeest horn begins its second bend these granulations momentarily follow a diagonal slew across the stem, corresponding with the "grain" on *Rabaticeros* horns. Ontogeny may, in this instance, hint at the phylogeny of the horns' growth and implies support for Gentry's assessment of relationships.

The reversal in horn direction at the *Rabaticeros* stage was accompanied by increased fusion of the two frontal bones along their midline septum and a wholesale elevation of the horn bases up from the cranium.

Disproportionate growth of the frontal bones has pushed in two directions: anteriorly it has served to depress progressively the muzzle until a nearly straight shaft of bone stretches taut from horn to nasal. The other principal developments in *Alcelaphus* are an increase in the weight of the horns and in their flexure. In this respect the living races exhibit a mosaic of characteristics; their simplest dimensions, length and circumference at the base can be rendered in tabulated form.

	Length (in cm)	Circumference (in cm)
<i>A. buselaphus buselaphus</i>	30—39	21—25
<i>A. b. swaynei</i>	40—51	22—25.5
<i>A. b. tora</i>	45—58	20—27
<i>A. b. cokii</i>	45—59	21—30.5
<i>A. b. caama</i>	45—70	23—33
<i>A. b. lelwel</i>	50—70	25—33
<i>A. b. major</i>	50—70	22—34
<i>A. b. lichtensteini</i>	45—62	25—37



Above in margin: *Parmularius* (*Damaliscus*?) fossil horn cores.

In text, from right to left: *Parmularius*, *Rabaticeros*, proto-*Alcelaphus*, *Alcelaphus buselaphus*.

The extinct race *A. b. buselaphus* appears to have had the shortest horns and pedicel: *swaynei*, *tora* and *cokii* have relatively slender horns, splayed sideways at the base and mounted on modest pedicels.

Horn clashing in *A. b. cokii* has been described by Gosling (1974a).

"The orientation of the horns of the two males during a clash was more stereotyped than in any other form of horn contact behaviour. The blow, delivered when both animals in effect fell forward from their hind feet, with the added impetus of the push from the hind legs, was taken entirely by the horizontal portion of the horns. The distal parts of the horns are displaced anteriorly and thus allow direct contact with the antero-dorsal surface of the horizontal portions of an opponent's horns. The blow is thus stopped above the head which is probably an important function of the horn shape in this subspecies of hartebeest. Immediately after the horns made contact there was a small but apparently vigorous twist of the head. Sometimes this was followed by immediate separation, the heads seeming to bounce away from each other with the force of the blows ... sometimes after a clash contact was maintained and males pushed forward, vigorously twisting the horns from side to side. This sometimes continued for long periods and often one or both males were forced up into a standing position ... Often during wrestling the head of one animal was forced to one side leaving its neck and shoulders potentially exposed to the horns of the opponent. When the clash occurred in encounters between females the horns of the two animals slid over each other in a variable manner. This is explained in terms of female horn shape: the horizontal portion of the horns are relatively oblique and the distal portion is not anteriorly displaced. As can be checked from manipulation of the skulls, the horns do not interlock as do those of the males."

Dropping on to the knees has an exact correlation with the stereotyped hammer-blow clash between well-reinforced horns. A low firmly based tripod is necessary to withstand the force of the blow. Fighting on the knees is rare and momentary in *Aepyceros* and, in *Beatragus*, is reserved for severe clashes only (R. Carr-Hartley, personal communication) but is universal in all other alcelaphines.

In *A. buselaphus swaynei* and *A. b. tora* the males, like *A. b. cokii*, have thicker and more hooked horns with the tip facing back rather than inwards or upwards as in the females. These intrinsically male characteristics of the horns are further developed in *C. b. caama*, *lelwel* and *major* where there are higher pedicels, thicker horns and the terminal hook faces straight backwards in both sexes.

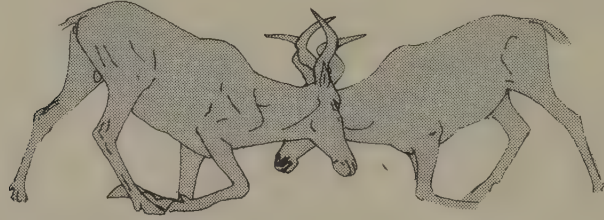
Inflation of the pedicel may be approaching its mechanical limits in the *lelwel* hartebeest, where the horns and their cores may weigh 3.75 kg and the horn cores branch about 15 cm above the orbits. The horns of *A. b. lelwel* are also the most vertical and least divergent of all races. During a clash between *A. b. lelwel*, the antagonists are further apart than in other races and the brunt of the blow is taken on the upper bends of the horns, hence the need for massive stems and broad boss-like bases. To wrestle the opponents link the terminal hooks and put the weight of their shoulders and necks behind scythe-like sweeps in which the head remains in the same plane as the neck; the animals remain on their knees, their horns tending to maintain continual contact with the ground. This is probably necessary because inordinate pressures must be exerted upon the upper neck by heavy horns being at the end of such a long lever arm.



Alcelaphus buselaphus lelwel.

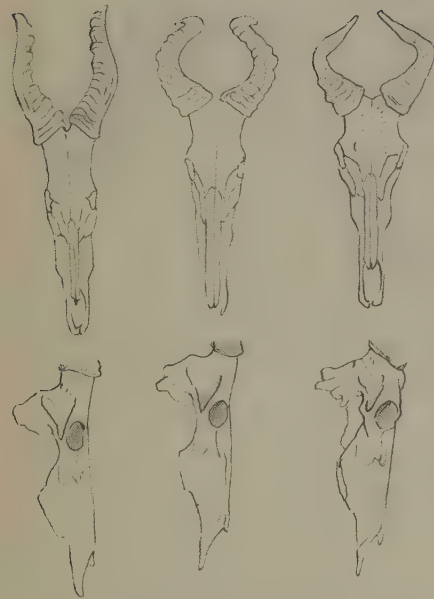
In spite of the mechanical advantage that the horns have gained it is associated with risk of stress or even dislocation of the axis-atlas junction. This may help to explain why long pedicels and upright horn stems have developed (and probably independently) in only two of the eight major regional populations. The range of a blow has been increased but the target area has narrowed.

Alcelaphus buselaphus horn wrestling.



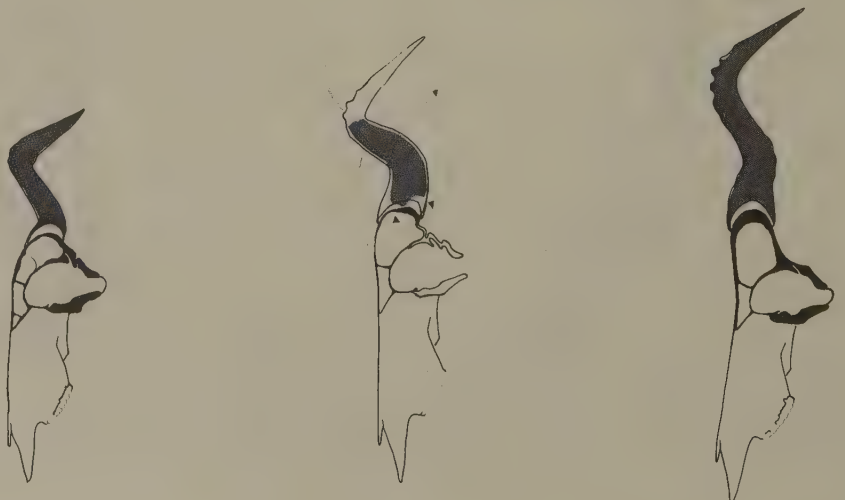
The disadvantages of a narrow defensive shield during clashes and of being restricted to a single plane of movement during wrestling is offset in the largest race *A. b. major* by a general widening and reinforcement in the crown. The pedicels are shorter and flatter, increased flexure of the horn bows them out to the sides, then in again and back. Greater versatility of movement is implied by lateral expansion of the occipital area. I have not been able to see this species fighting but such modifications suggest that the distance between combatants is shorter than in *A. b. lelwel* and the force of their clashes might be more concentrated. Strong lateral and fore-aft hooks provide two locking surfaces on each horn and imply greater dexterity during wrestling matches.

All these traits are carried much further in *A. b. lichtensteini*. From near the end of the Pleistocene at Broken Hill (Kabwe, Zambia) there are fossil horn cores with characteristics somewhat intermediate between *A. b. major* and *A. b. lichtensteini*. These fossils tend to confirm that the latter's more tightly curled horns have been compressed from a more extended condition



Above: frontal and lateral views of left: *Alcelaphus buselaphus lelwel*; centre: *Alcelaphus buselaphus major*; right: *Alcelaphus buselaphus lichtensteini*.

Right: cross-section of horn cores of (left) *Alcelaphus buselaphus major* and (right) *A. b. lichtensteini* with (centre) hypothetical intermediate skull. Fossil horn core from Broken Hill (shown in black) corresponds with intermediate form.



such as is found in *A. b. major*. The frontal sinuses have continued their retreat over the back of the cranium and have also flattened. The thick bony wall or septum that separated the pedicels before they deflated remains as a very prominent ridge on the forehead.



Alcelaphus buselaphus lichtensteini.

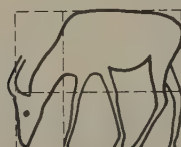
Migration of the horn cores in a lateral and posterior direction combined with a decrease in the sinuses is correlated with a broadening of the forehead and occiput. Superficially the morphology of these areas is not unlike that of the gnu but a closer examination reveals that the adaptive significance of these horn shapes is different. The flat plates on the forehead of *A. b. lichtensteini* show every sign of being deflated vestiges of formerly robust horn stems of *major* type and do not function as bosses as in the gnus. Instead, *lichtensteini* takes clashes on the upper loop of the horns as in *major* and *lelwel*.

Why should pedicels reduce in *A. b. lichtensteini*? The most plausible explanation is that an ancestral population of *A. b. major* type colonized the southern woodlands during an arid period following the Congo (Zaire) corridor that has been used by other mammal species (see Vol. I, pp. 65, 210; Vol. II, p. 420; Vol. IIIB, p. 317). The wide range of habitats and graduated zoning of vegetation belts south of the Sahara would have ensured that ancestral hartebeest populations would have been at least as dense (and probably much denser) in many areas of their northern range as they were when the region was first explored and described by naturalists in the last century. High densities involve high frequencies and intensities of combat. More offspring being the reward for the best endowed and most skilled fighters, there is strong selective pressure in favour of highly ritualized fighting behaviour and, I suggest, in the case of the hartebeest for an extended superstructure on the head.

When hartebeest from such a background invaded the southern woodlands they encountered a habitat laced with grassy glades and valleys, cumulatively an extensive habitat, but one that could only support hartebeest at much lower densities. At low densities the territorial males meet less often and there is much less selection for precision fighting.

If the evolution of more compact horns is correlated with very much lower densities and smaller, more widely scattered groups, then this certainly accords with the current ecology of *A. b. lichtensteini*. In all other aspects of its anatomy, ecology and behaviour *lichtensteini* is a typical hartebeest but being a large animal uneven contraction and shrinkage have had extensive effects on skull morphology.

Long faces are correlated with long legs in the alcelaphines. The relatively small, rather short-legged *Connochaetes gnou*, a relic species from the Cape has the shortest face of the "main line" alcelaphines. Even the impala is distinctly longer in the face than any gazelle, but it differs from the other alcelaphines in its long neck. Nonetheless, a gross difference between the musculature of the sexes shows that exceptional development of the males' neck muscles is necessary to power horn fighting and perhaps to compensate for mechanical disadvantages suffered by an over-extended vertebral column.



topi



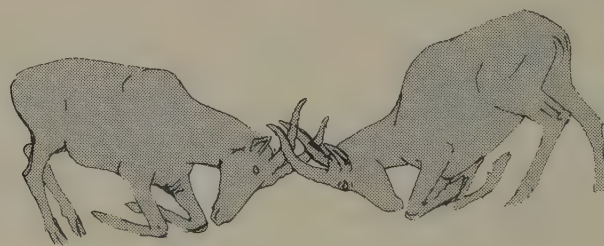
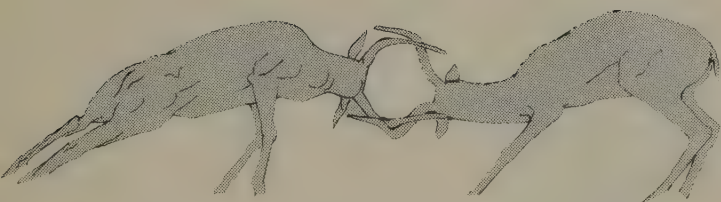
gnu

Ratio of shoulder heights to trunk and head lengths in *Damaliscus lunatus* and *Connochaetes*.

Table of actual dimensions for three species with similar shoulder heights show trunk and head lengths increase with body weight.

	<i>Damaliscus lunatus</i>	<i>Alcelaphus</i>	<i>Connochaetes</i>
weight	135 kg	160 kg	200 kg
shoulder height	125 cm	130 cm	130 cm
trunk length	100 cm	120 cm	128 cm
condylobasal length	39 cm	42 cm	50 cm

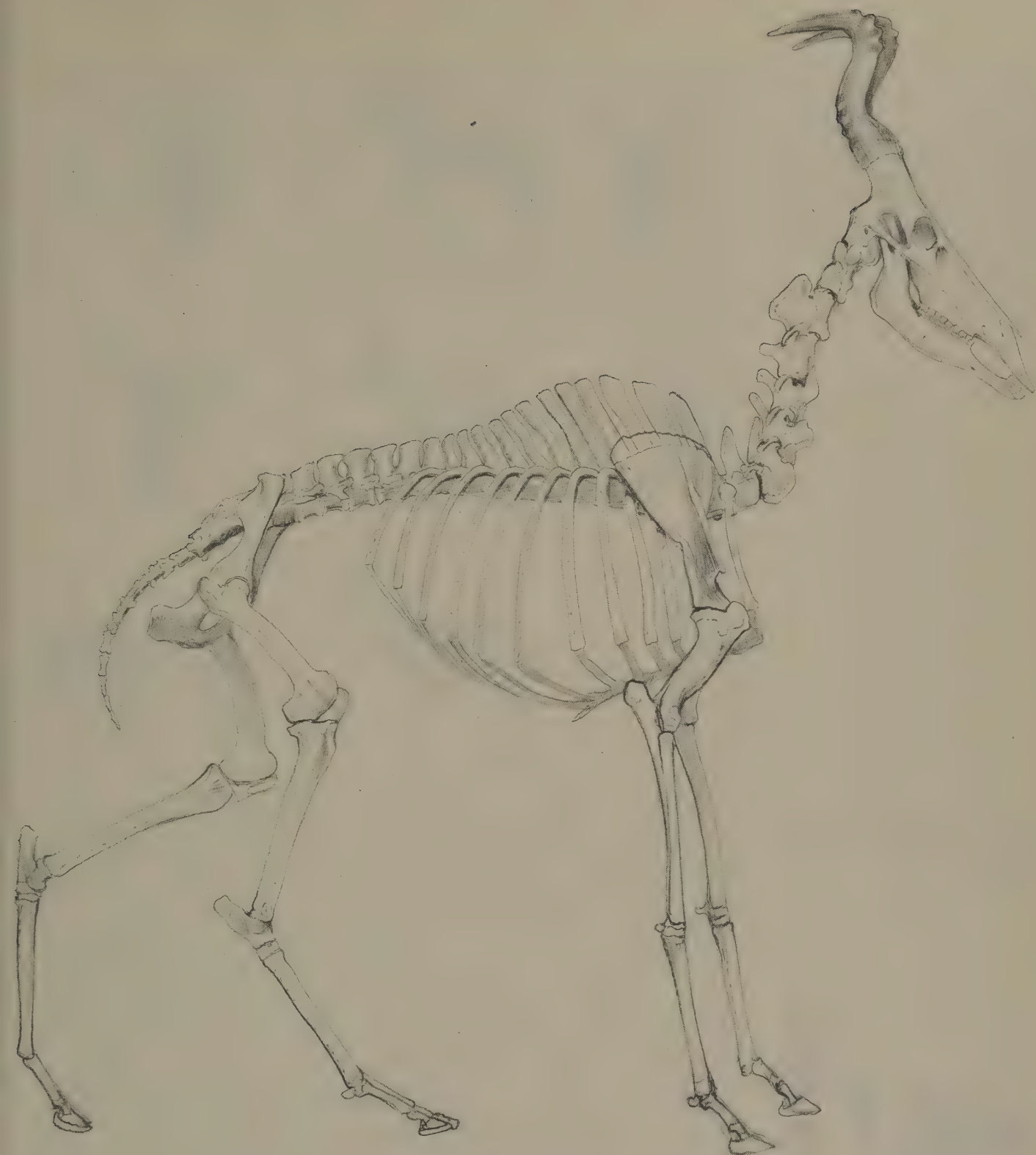
While greater size lengthens the distance between body and ground and should favour lengthening of the neck, intraspecific competition favours an opposite trend; a short thick neck being better for fighting. In a group of antelopes where both sexes establish rank orders by fights or threats and females must also protect their offspring from intolerant adult males, the answer has been to elongate the head rather than the neck.



Fighting impala, *Aepyceros* and topi, *Damaliscus lunatus*.

As a solution to one of the problems posed by increasing size, shortening the neck and lengthening the face has so altered the proportions of the alcelaphines as to further obfuscate their antilopine origins.

Interspersed with such major transformations the alcelaphines show some curious instances of conservatism. Body products, glandular secretions



and the rituals in which olfactory communication is used do not differ very greatly from those of some antilopines and neotragines, except that pre-orbital secretions are used to mark the body more than to label the environment, a change in emphasis that reflects the enlarged scale of the alcelaphines' world. Pedal glands and scent-trailing are well developed. Dung

Alcelaphus buselaphus lelwel.

Retention and transformation of pattern elements in alcelaphines compared with, top left, a gazelle (typified by *Gazella soemmerringi* and, top centre, a generalized antilopine. Black-faced impala (left centre); topi (top right and centre); red hartebeest (left and centre bottom); brindled gnu, right, middle and bottom.



Below: Mud, ash and "grease" pattern on a male *Alcelaphus buselaphus leltwel* showing absence of staining on rump.



middens and an interest in such scent posts are universal in the Alcelaphini. The ears of all species are little different from those of Antilopini. The tails of *Damaliscus* and *Alcelaphus* are haired like those of gazelles (*Beatragus* is more like *Aepyceros*). Even more striking is the manner in which coat markings, which are often precise and geometric in the Antilopini have, in the Alcelaphini, been distorted or suppressed altogether. The pygal, flank and facial stripes that are so common in gazelles and springbok are retained, but in a highly modified form, by *Damaliscus* and some races of *Alcelaphus*. The distribution of these markings has a remarkable coincidence with the pattern of self-anointment. Facial or preorbital glands are functional in all alcelaphines: territorial males may mark the occasional stump, termitary or grass stem but often follow it by rubbing with the forehead and direct anointment with secretions is the main use to which the glands are put, making the animal, particularly a territory holder, into a walking or standing scent-post. In all species and both sexes animals tend to take up positions on termitaries where by simply standing they can signal status and tenancy. It is perhaps significant that these behaviours are most highly ritualized in territorial males of *Damaliscus* and *Alcelaphus*, the genera in which markings can most look like greasy smears on the upper legs; sudden movements of the head not only mark the shoulder or flanks but "point" to these

significant areas. Black is an optically assertive colour and its coincidence with areas of scent suggests that conspecifics will be selectively sensitive to such marks. When a topi stands on a termitary or leaps into the air during a challenge or cavorts, the configuration of black markings certainly enhances the visual impression of verticality (culminating in the horns), but this is probably a subsidiary effect to the function of advertising scent marks. It has also been suggested that coat colouring in *Alcelaphus* and *Damaliscus* may be influenced by physiological considerations or thermo-regulation (Finch, 1972a) and it is interesting that the brown colouring on a topi lies above areas of thin subcutaneous muscle, while the black patches coincide to a large extent with muscles that are not covered over by these thin muscle sheets.

In several localities individual topi have been recorded with white instead of black markings exhibiting thereby prominent white blazes on the forehead and upper limbs and a white tail. The blesbok, *D. dorcas*, has just such a blaze on its face and white lower legs, a heightening of conspicuousness that may be correlated with enhanced value for ritualized head-flagging in the blesbok's communication system.

The unpatterned subspecies of *Alcelaphus* appear to have suppressed pattern by simply retaining the cryptic infantile colour throughout life. The present situation is no guide but it would appear that *A. b. swaynei* and *A. b. caama* shared with most populations of *Damaliscus* and *Connochaetes* the distinction of living at very high densities, the former hartebeest on the Haud Plateau, the latter in the Cape. Signalling devices may have declined in importance where densities have tended to be lower and predation becomes a larger consideration than social communication.

Even the brindled gnu retains vestigial markings on its upper legs, and the black bridge of its nose has become a tarry scent brush serving to dispense scent from the preorbital glands. It is arguable whether irregular brindling of the forequarters looks more like greasy skin folds or an extension of the lank mane hair. A mane, beard, long horse-like tail and sideways splay of horns have combined with shorter, stockier proportions to transform the gnu into the parody of a miniature bison; so much so that L. S. B. Leakey, among others, was convinced of its bovine affinities.

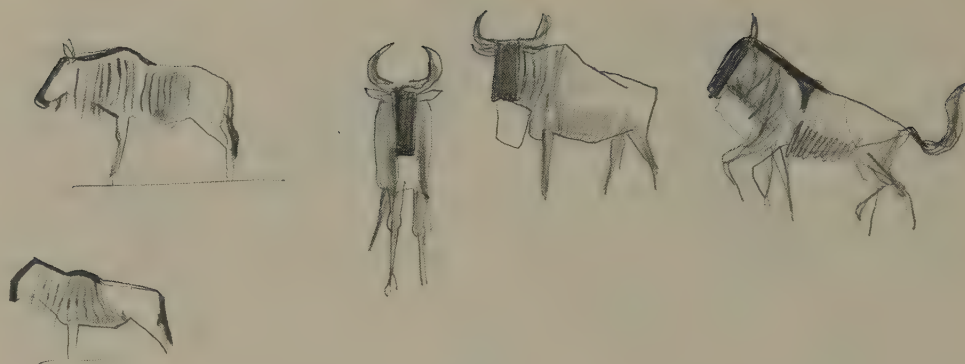
Why should the gnu look so different?

That tail lashing has been especially elaborated as a social signal is evident in the brilliant white tail of the black *Connochaetes gnou*, but *Connochaetes taurinus* has a black tail and mane, and this advertises movement rather than providing a visual colour contrast. It is as though movement has acquired a primary signal value.

If the gnu's ritualized behaviours are compared with those of its sleeker relatives, there are several static or slow activities in the latter that are mobile or fast in the former. The most conspicuous of these differences concerns territorial behaviour. Hartebeest or topi territorial males tend to interact with their neighbours by walking towards one another with nods or lateral flagging of their hammer-shaped heads, their vertical horns amply advertised, particularly in profile view. In the gnu, which from a side view shows very little horn, there are the same basic sequences but movements of the head become jerky eye-catching tosses because the animals, rather than walk,

Left: *Connochaetes taurinus johnsoni*
static advertisement of territory.

Right: *Connochaetes taurinus albojubatus*
mobile advertisement of territory.



will canter in a ritualized manner towards one another. Instead of playing out a slow and frequently static ritual on an established meeting point gnus tend to be much more active. Swinging their heads and lashing tails about they will roll on the ground and often set off at a gallop upon boundary-beating excursions. (These “cavorts” are described on p. 531.) When a male herds or attempts to coerce females into remaining within his territory he does not simply block their path with a static broadside posture but will often prance and leap, twisting so as to put his flattened profile and flouncing tassellations to best effect. Although the higher energy budget of the gnu could have an influence speeding up such behaviours, it is more likely to be symptomatic of increased levels of intraspecific competition and the need, literally, to stand out in a crowd; cavorting therefore augments the evidence for the gnu’s adaptations being geared to high densities.

Adaptation to high density is not only related to its own species. So dependent is the gnu on short lawns that it obtains positive benefits from mixing with voracious feeders like the zebra, particularly during seasons when the grass is growing and full of nutrients but soon goes beyond a croppable height (see Vol. IIIB, p. 140). The very short broad mouth is well adapted to crop grass but is ill-suited to cope with tall coarse stems.

By contrast, the hartebeest has a narrower mouth with a larger gape and the most hypsodont teeth in the tribe. Although adapted to very coarse diets, *Alcelaphus* and *Beatragus* are unable to colonize truly arid land: even the extinct North African race only occupied moister fringes of the Sahara. All Alcelaphini tolerate exposure to intense radiation but are dependent to a greater or lesser degree on water or at least on moist foods, and this is consistent with the group’s early derivation from a less arid-adapted branch of the Antilopini.

The living species show a dietary gradient which was well recognized in Hofmann’s (1973) correlation of stomach structure with feeding habits. He classified the impala as an intermediate feeder preferring grasses, the gnu as a fresh grass grazer that is dependent on water and the hartebeest and topi as roughage grazers.

Both *Connochaetes* and *Damaliscus* tend to die out when numbers get very low; for the gnu this may be partly dietary in that they are not adapted to graze in long grass, but isolated individuals are also conspicuous and easy



Gnu, *Connochaetes taurinus*.

targets for predators, the young being especially vulnerable. This is another indication of their adaptation to high densities. Another is the frequency with which these alcelaphine types occur in Pleistocene fossil deposits (where they are the commonest bovid tribe).

All the alcelaphines have specialized ecological requirements. The impala has a fairly catholic diet but is intrinsically an "edge" species, living on the boundaries between woodland and grassland. The hartebeest is also an ecotone species but has lost the dietary versatility, being exclusively a grazer. Where there are numerous short grass grazers, particularly gnu, hartebeest tend to be pushed further into the more wooded savannas. Where this pressure is absent, they may become dominant in open grasslands but Gosling (1974b) pointed out that they always retain contact with woodlands and are most characteristic of fragmented valley systems where catenary belts of vegetation, particularly different grass types are close together; here individuals can establish home ranges that meet their needs for most of the year. They therefore tend to be more residential. *Damaliscus*, instead, only occurs in very large valleys or sumplands where enormous seasonal resources are available as floods come and go. The damalisc must make seasonal movements to exploit such resources and, when the pattern of rainfall and flooding is in their favour, they can reach very high densities. Population cycles with build-ups and crashes are therefore common. If the hartebeest is absent from the margins of a topi population centre the latter may fill the hartebeest niche and follow a similar type of ecological dispersal pattern in small territorial groups. The gnu, which is peculiarly dependent on homogenous areas of short grass, can in some areas find such conditions within a small compass throughout the year, but such resources are generally limited and likewise limit the density of gnus. Where there are very large separate areas of homogenous and seasonal short grass grazing, as on the Serengeti plains, the gnu must move and can achieve huge numbers.

The hirola is a coarse grass grazer but is a relic species, having very probably been replaced by *Alcelaphus* after being a dominant occupant of this niche earlier in the Pleistocene.

Most alcelaphine species are able to select for plant parts by raking grasses through the mouth. They regulate their intake by controlling the breaking point of the leaves or stems. The damalisc in particular modifies its cropping technique according to the growth stage of the grass. Tactile discrimination between distasteful and palatable plants is augmented by taste; the latter a facility that might be partially learned. For some time after weaning, hand-reared damaliscs that have been introduced to new and well-favoured foods repeatedly probe their nostrils with the tongue while inhaling, (Bonarius, personal communication).

The distribution and type of food determine activity patterns and, as grazers, all alcelaphines have long rumination periods. They are predominantly diurnal animals and visual modes of communication are highly developed. Tail movements, alterations in the angle of the body, head, horn,



Hirola, *Beatragus*.

ear angles provide a semaphore of signals. The combination of an intensely social life with much competition (particularly among males) and the fact that these are some of the fastest most mobile of bovids means that a number of displays take place at the run; ritualized gaits and postures are therefore common.

Grass is a very much larger and more generally available but more rapidly changeable and ephemeral resource than browse: the grazing alcelaphines are therefore capable of achieving "much larger numbers than browsers but are more vulnerable to seasonal or longer cyclic changes. Some of the implications of this for the social life and population dynamics of herbivores have already been discussed in the bovid profile, but two particularly important effects for the alcelaphines should be mentioned.

Having inherited a sedentary, territorial type of organization, all species have sedentary, territorial phases or populations but they are also forced to make nomadic movements in other phases or in other parts of their range.

In the second condition, temporal and spatial differences in the abundance of food also induce enormous changes in population density from one place and from one period to another. Being related directly to the adoption of grass as a diet, these pressures on the alcelaphines must have been influential factors from the earliest stages of alcelaphine evolution. The result appears to be exceptional versatility in social organization.

In all species both males and females become attached to a limited locality if ecological conditions permit it. Both sexes may exclude strangers in stable sedentary situations and, where there is year-long food available within a small compass, permanent male territories and female home ranges are maintained; a semi-closed membership of small groups may even develop. Where the relief is broken and narrow belts of vegetation allow each species to meet its requirements in a restricted locality somewhere within the mosaic, alcelaphines will space themselves out in appropriate areas. Females tend to cluster on the best patches and male competition ensures that the strongest males monopolize these patches by forming territories in which access to females by other adult males is excluded.

It is food that ultimately determines where females are and how sedentary they can be but it is the strongest males which have won territories in preferred areas that have the best chances of detaining females and mating with them. Both sexes may be sedentary if the vegetation and climate allow it and a scattering of small, relatively stable groups of females will live permanently within the network of territories. The stability of their membership depends on the frequency of their contacts with other groups and the success of the male in restricting them to his territory.

Since extensive swards of short grass tend to be impermanent in broken up mosaics of vegetation this pattern of land tenure is rarest for the gnu. It is less rare for topi, which tolerate grasses in a wider range of growth stages. It is the commonest, indeed the normal pattern, for hartebeest which most easily find their preferred forage by moving up and down a catena composed of narrow vegetation belts. The only detailed study of hartebeest has been of a fairly dense resident population with breeding monopolized by territorial males and distributed throughout the year (Gosling, 1974a). My own more superficial observations of a seasonally breeding and nomadic population in Karamoja suggested that animals were forced off their territories by drought and selection had concentrated their breeding to enhance survival of the young.

Major differences between hartebeest and topi originate in their dietary

preferences and the scale of their movements in pursuit of food. While hartebeest tend to be dispersed in partially wooded small valleys topi are most successful in very large valleys where they move *en masse* between wet and dry season pastures. In more confined but moister habitats they may follow a rotational cycle with more or less continuous movement. Gnu are also most successful in extensive homogenous habitats where they can move in large groups.

Wherever alcelaphines breed seasonally the males tend to show gross seasonal changes in behaviour, becoming mutually intolerant or territorial during the rut, while they tend to become gregarious at other times. In nomadic populations the onset of oestrus in females seems to activate these changes. When this happens while gnus are on the move between predictable traditional pastures, as it does in the Serengeti National Park, males set up very small temporary territories in the pathway of the nomads and attempt to alternate chasing off other males with the arrest and mating of oestrous females. In similar circumstances topi have been seen to set up temporary territories, but at Ishasha, where the topis' opportunistic movements are relatively unpredictable a majority of the dominant males maintain contact with the body of the herd by continually altering the area of their activity. Effectively, the temporary territory becomes a moving territory or, as Jewell (1972) has called it, a "ward". Yet another pattern emerges when large herds make predictable movements on traditional seasonal pastures. Like the gnu, males that live and move in companies for the rest of the year suddenly become mutually intolerant. In this manner large concentrated groups of males become temporarily territorial, but the event differs from its gnu equivalent by being more restricted in time and space. So predictable is the annual cycle in areas of high topi density that the territorial clusters always tend to form in the same locality (Monfort-Braham, 1975). At the time of their change in status the temporary territorials are in any case likely to be at the centre of female activity but the exact placement of the territorial clusters may be refined by many years of repetition. The clusters appear to occupy very strategic points such as the juncture of two streams (which can act as the walls of a funnel), or they are close to the head of a promontory around which the herds regularly pass or simply in the centre of a major pasture.

Monfort-Braham thought that the males on territorial clusters probably achieved a higher proportion of matings than the more widely spaced territory holders in the surrounding country. In all alcelaphines behaviour tends to be drawn out, relatively elaborate and ritualized when courtship takes place on an isolated territory. In crowded situations, whether in "wards" or in temporary territories, the preliminaries are absent or abbreviated and, in general, behavioural differences may be greater between high and low density populations of the same species than they are between different alcelaphine species.

In topi herds the females actually seek out the clustered males. What then has happened to reverse the usual pattern where females are relatively passive objects that attract male activity? The reversal is all the more intriguing because it only happens when topi are at very high densities and even then only in some localities.

Monfort-Braham's observations on topi, those of Watson (1969) and Estes (1969) on gnu and of Warren (1974) on impala suggest that vocal signals have come to assume a large part in the social and particularly in the sexual behaviour of these species. An animal's ability to respond to stimuli is drastically curtailed in a large herd and functional signals have to be in an appropriate mode and be grossly exaggerated to be effective. The range of visual signals is severely contracted, olfactory signals are easily swamped and auditory signals, which have the greatest potential range, cannot be subtle in a crowd. The bovid bleat has therefore been jazzed up into a roar or a very loud grunt. In all alcelaphine species high densities can be correlated with an increase in the frequency of male auditory signals. Furthermore there is a phylogenetic dimension in that the species with the largest herds have the loudest calls.

The loudest calls are essentially an advertisement of male hormonal condition and dominant status. In impala, topi and gnu, males are extremely vocal in their relationships with females, particularly when they live at high densities; greeting, inspecting, herding and mating are all accompanied by loud and continuous noise. Females submit to approaches and copulations of an abruptness and noisiness that would frighten off the females of many other antelope species. In Akagera, Monfort-Braham recorded herds of several hundred topi females repeatedly drift across a cluster of territories. She also observed females abandon their herds in small groups and make brief visits to the trampled foodless arena of a territorial cluster at which time many were mated. All such visits are attended by much noise and activity on the part of the males: the clustered males must also emanate a powerful scent.

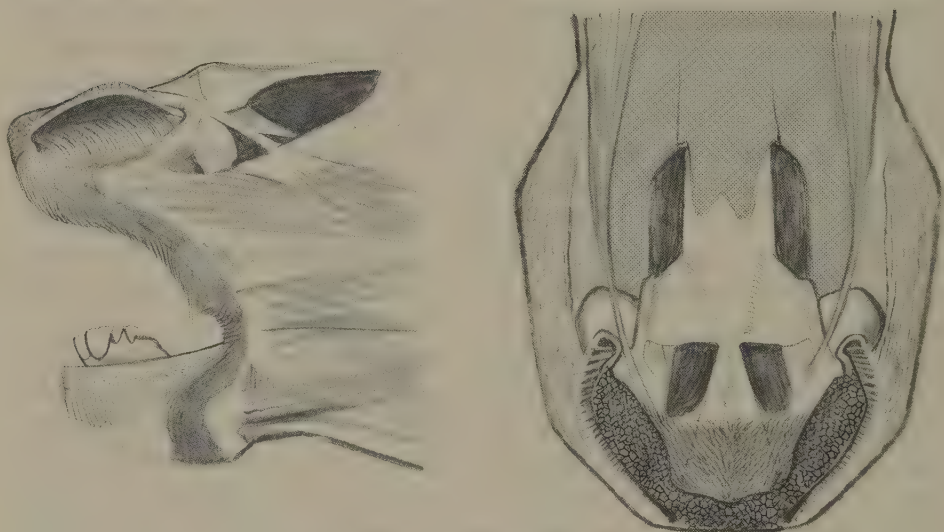
Impala females also appear to be positively attracted towards roaring males during the mating season but there could be a major difference in incentive between the oestrous impalas' attraction to a roaring male and the topi females. Since the roaring is simultaneously an intimidating signal to other males, the roarer may be offering a haven to impala females from persecution by bachelors. The intimidatory effect is however more questionable in topi where the females, being horned, are quite capable of fending off unwelcome males. Neither of the two major incentives, food or protection, can attract a female topi to males on territorial clusters.

I think it is possible that a reduction in the repertoire of signals and an increase in the volume and relative impact of the remaining signals may be matched by stronger responses in receivers. This could help explain heightened response to male signals in females from big herds. Gross phenotypic differences in intensity of oestrous behaviour are well known in domestic bovids, where the strongest manifestations of "heat" are usually associated with much vocalization, restless wandering and spontaneous solicitation of males or "presenting". Amplification of the male's sexual call and its multiplication (probably augmented by scent), may help to bring about a similar intensification of female sexual behaviour, providing a mechanism whereby the insemination of all females in a mega-herd is ensured. These considerations may apply in greater or lesser degrees to reproductive behaviour in high density herds of all alcelaphine species.

Discussion of the relative importance of social and environmental stimuli and whether female cycles are influenced by stimuli emanating from the male and vice-versa follows in the species profiles. At present this is a highly speculative area but with appropriate techniques and tools it is one with rich possibilities for future research and with important implications for our understanding of the full range of possibilities in bovid reproduction.

The implications of high density living in the alcelaphines are much more extensive than can be suggested in a brief profile but I should mention a feature of the topi and gnu that might be directly adaptive to the dust generated by big herds. Both species have wide flattened, hair-lined nostrils with a peculiar cartilaginous pocket or baffle in the back corner. The nasal area is less highly specialized in the hartebeest. The extremity of the nose probably retains some facility for evaporative cooling of venous blood in spite of the distance between nostrils and brain having been greatly extended.

Dissection of the nose in *Damaliscus lunatus*. The cartilaginous extension of the nasals has two domes behind the nostrils which are contiguous with invaginated cartilaginous pockets just below.

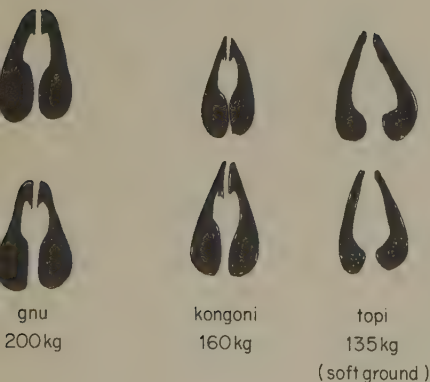


The hooves of alcelaphines show some modifications consistent with their weight and the nature of their normal substrate. Frequently confined to water-logged habitats, the topi has the longest, narrowest hooves, the heavier gnu has the roundest and broadest while the hartebeest is intermediate.

The periodicity of alcelaphine breeding is highly responsive to local conditions. Continuous breeding, poor or well-marked peaks, regular seasons or irregularly peaked echelons have all been recorded and, in the case of topi, all in different populations of the same species.

The exigencies of nomadic life have forced the infant gnu to stand, run and keep up with its parent within hours of birth but this is the only exception to the normal antilopine pattern of the young "lying-up" for the first month of life; topi, however, vary in the time spent in hiding. Most gnu births are very strongly seasonal, and Estes (1974) considered that the swamping of predators with a glut of calves might serve to increase the overall survival rate.

Alcelaphine hoof-prints.



Except for the gnu all newborn alcelaphines are a cryptic fawn colour for the first couple of months of life. Lactation lasts less than six months. Horns appear before they are three months old and growth is very rapid. Both territorial and bachelor males tend to attack young males from an early age and the horns and defensive behaviour of mothers are very necessary to the survival of their male offspring.

Sexual and social maturity are variable from species to species and also from one population to another. Gosling (1974b) recorded male hartebeest remaining with their mothers in a non-reproductive condition for up to three years. Noting heavy predation in "early leavers" (partly due to the intolerance of older bachelors), he interpreted the mothers' shielding influence as an adaptation that gave the maturing male access to resources which would otherwise be denied to him. Topi and gnu males tend to lose their mothers by the time they are one year old and in such cases new calves are the beneficiaries; whether this is the product of a weaker maternal shield or a stronger male drive is difficult to determine.

Variations in the age of first copulation or conception probably reflect nutritional and density-dependent controls.

The alcelaphines are one of the most successful and highly versatile of all bovid groups; however their productivity and adaptability to high densities has not saved some populations from near-extirpation. These facts give them a high priority for more intensive conservation as endangered species or subspecies, for greater efforts at rational exploitation and for further research. Extirpation or reduction of alcelaphine populations to dangerously low levels in northern, north-eastern and southern Africa should be a warning that members of this group are especially vulnerable to hunting, the destruction of their habitats and in some cases to excessive competition from livestock.



Impala
(Aepyceros
melampus)

Family

Bovidae

Order

Artiodactyla

Local names

Swala pala (Kiswahili), Eswara, Iswala (Luragoli), Ipara (Kijita), Empala (Luganda), Mhala (Kisukuma), Chebotewerer (Kalenjin), Entarakwet (Masai), Etarawet, Ndaraguiti (Kikuyu), Nkoperai (Samburu), Nyakech (Lwo), Akopolae (Turkana), Ndartai (Kikamba).

Measurements
head and body

135 (115—144) cm females

145 (125—154) cm males

height

70—85 cm females

75—92 cm males

tail

24—40 cm

weight

45 (40—53) kg females

60 (53—76) kg males

horns

45—91.7 cm

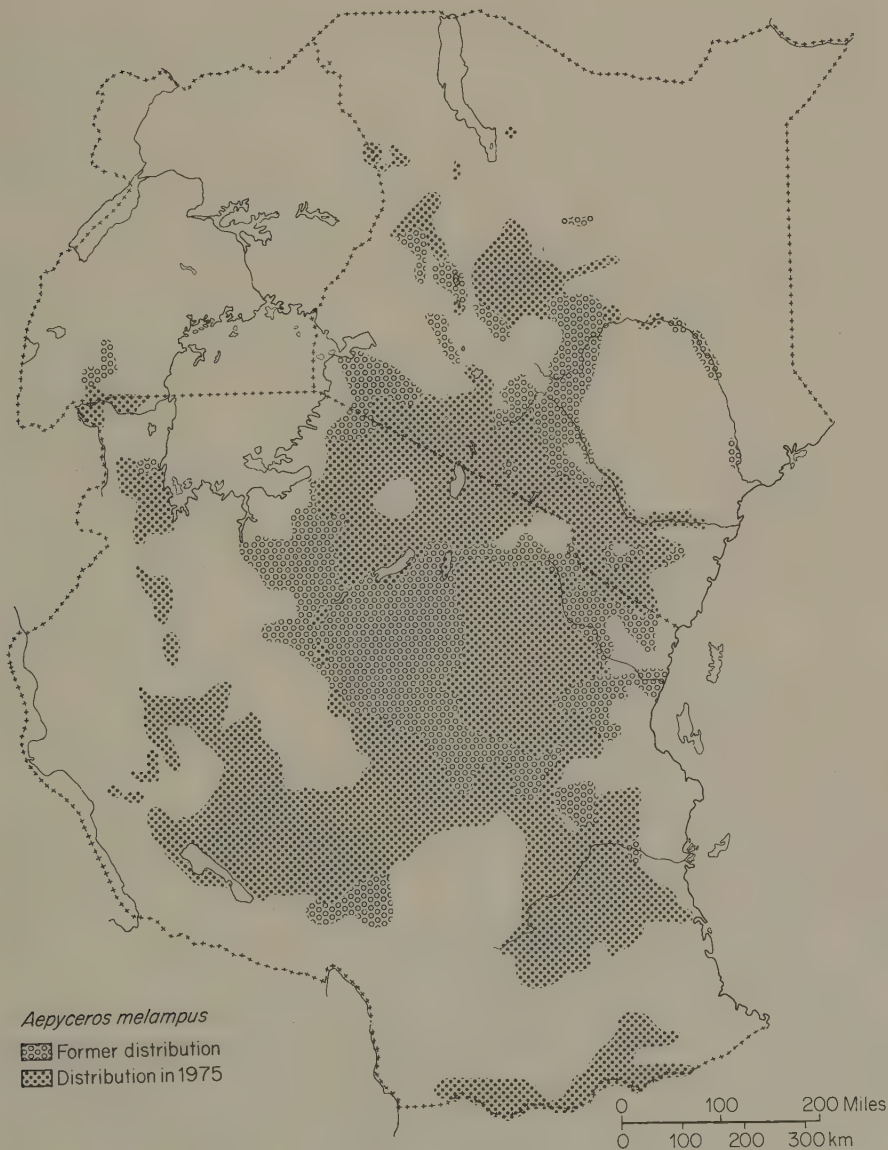
Note: There can be regional differences of up to 6 kg in average weight.

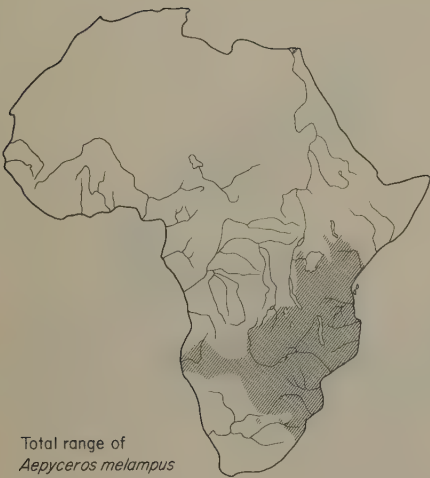
Impala

(*Aepyceros melampus*)

The impala has the proportions and general demeanour of a large gazelle but many details of its anatomy and behaviour show that it has diverged very widely from its antilopine origins. The significance of these divergences may be related to two unusual features of the impala, its gregariousness and the inclusion of relatively dense bush in its habitat.

The impala's range approximates to the boundaries of what I have described as an ecological "overlap" zone in eastern and south-central Africa (Vol. I, Preface). Within this zone the impala's habitats are neither arid





Total range of
Aepyceros melampus

and open nor stable and permanently wooded. In East Africa they prefer acacia and other deciduous woods and bushlands. These communities often form strips in between open grasslands and denser woodlands. In places, "edge" habitats, notably acacia savannas may be so widespread as to be the major vegetation types over extensive areas but this does not conceal the fact that impala are irregularly distributed and have special requirements, particularly good quality fodder, in both open and closed habitats, water and shade. Noting their dependence on water, Skinner (1978) has suggested that impala evolved on the moister, eastern side of Africa.

Considering the most likely course of impala evolution, open areas should be closer to the ancestral habitat, and movement into dense woodland is probably a secondary adaptation with food and shade the major incentives. This straddling of an ecotone may therefore have simple dietary and physiological explanations but the broader implications for the animal's biology are more complex.

The impala has an advantage over species that are more narrowly constrained by diet and habitat. Able to graze and browse, use of both grasslands and woodlands means that food is more seasonally reliable and the overall supply is hugely extended. Implicit in this dietary advantage is the potential for greater numbers, and there are grounds for interpreting some of the impala's peculiarities as the product of a very early adaptation by gazelle-like antelopes to higher densities.

Living in open environments gazelles and springbok use visual signals for communication and have conspicuous patterns and appropriate ritualized postures and behaviour. By extending its range into densely wooded country the impala has diminished the value of visual signals and there has been secondary reduction in conspicuousness of the coat pattern. The impala's colouring is extraordinarily similar to that of the gerenuk, another thorn-bush dwelling gazelline, but the former's black thigh stripes resemble a smaller-scale, short-range version of those found on Grant's gazelle and their function is, I suspect, identical in that this highly social antelope has a wider radial angle within which it can transmit a rump signal by mimicry of the black genital cleft on the thighs.

Visual communication remains important for the impala, particularly at short ranges, but contact in closed habitats has required the elaboration of unique olfactory and vocal signals. The "personalized" and fixed olfactory markers of a stable territorial system have been replaced by a vocal advertisement of male status. The male skull and larynx have been modified to amplify a weak antelopine bleat into a loud roar that carries well but does not seem to show individual variation. Resonance might be assisted by the empty sinuses that fill the space between orbits and palate. Female skulls show less of this pneumatization of the maxilla and females are unable to roar. It will be suggested later that the evolution of the roar is correlated with a decline in territorial behaviour.

Between the maxilla and premaxilla, impala share with *Neotragus* species the distinction of a large vacuity (see p. 176). The phylogenetic origin of this peculiarity appears to be identical in both species in that it correlates with a secondary elongation of the nasals and premaxilla and a diminished need for sophisticated heat control in better watered and shaded habitats.

The window has apparently come about through the freeing of the upper connexion between maxilla and premaxilla so that the latter could travel up to make a solid joint with the nasal.

This development is another indication of the impala's evolutionary history. In the heat-adapted gazelline and antidorcine antelopes there is no firm contact between the rather papery nasals and premaxillae. In impala males, which are larger, longer-horned animals, the muzzle has well-knit compact bones and there is no trace of preorbital glands. Although the modern impala has totally lost these glands and the lachrymal pits to contain them, there were smaller impala, living nearly four million years ago, which had vestigial preorbital pits (Gentry, 1978a). Progressive reduction of these facial glands is likely to be part of a general suppression of modes of communication that were originally adapted to primitive, low-density spacing systems.

Some glandular activity remains in the skin of the impalas' forehead, and traces of the secretion can be detected, particularly in adult males. The motor pattern of rubbing the face on vegetation is also discernible in dominant impala males in situations analogous to those typical of territorial antelopes (before, during or after an encounter with other males, females, or after defaecating) but the same bushes are rubbed by different males. Schenkel (1966a) also saw bachelors face-rub occasionally and in peaceful situations where their neighbours made no response. Tree-horning, which is a closely related activity and one of symbolic importance for several neotragine and antilopine species, is common but elicits no response from other impala and Schenkel recorded it equally in dominant males and bachelors.

In territorial species glandular marking and horning of vegetation are combined with dung piles and defaecation rituals to demarcate exclusive boundaries. Dung piles are used, mainly by impala males, but their siting is without frontier significance and in Sengwa, Zimbabwe, Warren (1974) found that several (perhaps any) males can contribute to them. Furthermore, excretion is not usually accompanied by ritualized social behaviour involving other animals. Warren observed that middens provoke addition from neighbouring males rather than avoidance and he suggested that they might simply serve as "olfactory listening posts".

The vestigial nature of impala glandular marking and of territoriality was evident in a study of impala in the Serengeti National Park (Jarman, 1973). She found that dominant males spaced themselves out in a mosaic of ill-defined territories. Not only were the areas poorly demarcated but males tended to shift the focus of their activities in conformity with the movements of female herds. Furthermore she found that the current alpha males might share their strong attachment to small localities with other males. Such males, generally gathered in bachelor groups, were tolerated by the alpha males if they kept away from female herds and showed subordinate behaviour. Within the bachelor groups Jarman was able to identify hierarchical orders and she followed the progress of individuals up to the point where top animals actually challenged territory holders in fights. She also recorded the re-entry of ex-alpha males into low ranks of the hierarchy.

How long an animal can sustain alpha status depends on the number

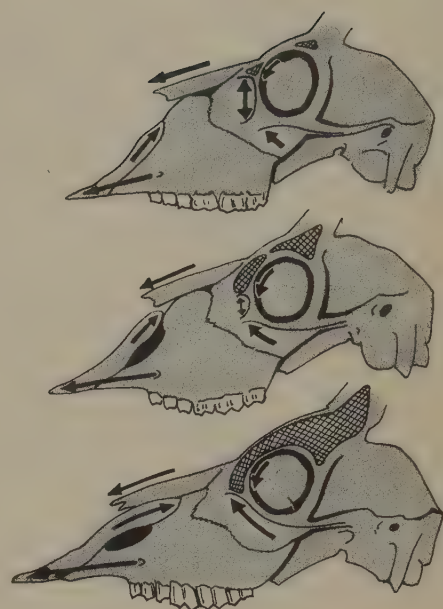


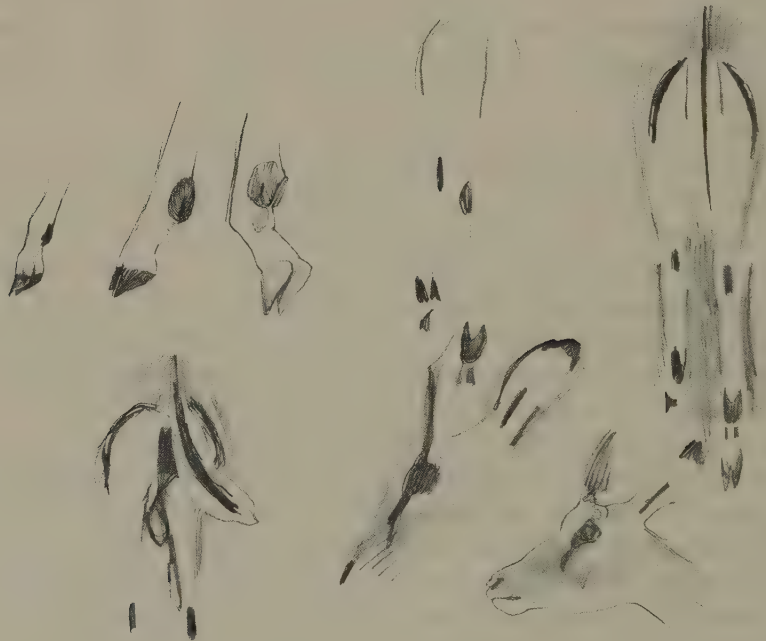
Diagram suggesting changes that have modelled the impala's skull (bottom); from gazelline-type skull (top); Arrows show shallow masticatory muscle attachment, large preorbital gland, loose nasal and short face. Hypothetical intermediate skull (middle) shows effects of extending masticatory muscle attachment, inflating forehead, diminishing gland, lengthening and strengthening muzzle.



of potential challengers, the number of females to be herded and the temporal intensity of the rut. The more competitors a male has to dominate or chase away and the more females he has to herd the faster will he be exhausted, so that his tenancy may last only a few hours in a very crowded situation or a matter of months where the population is less dense.

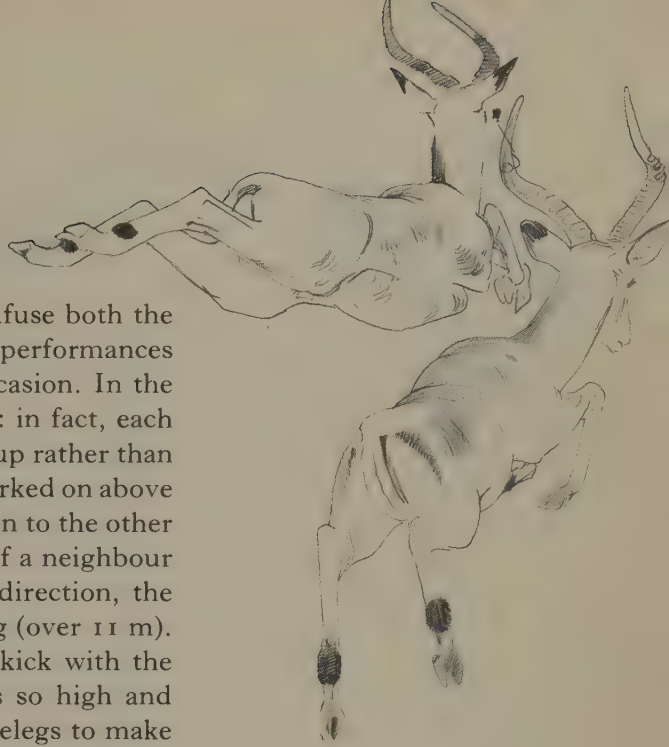
It has long been known that animals tend to abandon territories and form dominance orders when space is restricted and numbers are high (Shoemaker, 1939; Crowcroft, 1955). For the impala this progression could have an evolutionary dimension. If high densities were normal for very early ancestral populations there could have been strong selective pressure in favour of behaviour appropriate to such social situations and against pre-existing structures that were inappropriate. That impala have long been successful and numerous is implied by their abundance in the fossil record since the Mid-Pliocene.

Another unique feature of the impala can be directly related to their gregariousness and their movement into denser habitats. Both sexes possess highly conspicuous glands on the fetlocks which are unique to the species. Maintaining or establishing contact in a bushy habitat can be problematic and the fetlock glands are clearly of considerable importance in laying a trail which any temporarily detached individual can pick up and follow.



For the human observer, a familiar view of impala is of leaping animals scattering through the bush at his approach. Numerous descriptions have been published of this magnificent spectacle and all have emphasized the confusion of the scene: many authors have believed that leaping confuses predators, particularly because of the visual effect produced by the markings.

Fetlock glands apparently expanded during jumps (from photograph.)



The leaping and jinking from side to side may very well confuse both the predator and human observer, but close observation of these performances reveals that certain action patterns are repeated on every occasion. In the first place, the jumps are by no means a wild panic reaction: in fact, each leap appears to be oriented towards other members of the group rather than being a direct product of fear or alarm. The side jumping remarked on above is a conspicuous feature; each animal leaps to one side and then to the other very often passing over the back or cutting across the front of a neighbour in the process. Quite apart from their tendency to change direction, the impala's leaps can be both very high (over 3 m) and very long (over 11 m). The high jumps are often followed by a last moment high kick with the hindlegs just as the forelegs touch the ground. The kick is so high and vertical that, to avoid a somersault, it is necessary for the forelegs to make a double pace forward before the hindlegs can get down to the ground again. Visually, the effect of this violent twitch of the hindlegs is of a rocking leap ending in a bounce, a gait that is unique to the impala (see drawing).

I have isolated individuals with a Land Rover in order to test the zig-zagging reaction and found that the pattern of alternate movement from side to side was consistent even when the animal had been herded out of sight of its fellows. The movements may take the form of alternating individual leaps or a general swing or run to the left and right.

An initial explosion of excited impala is the product of each animal running randomly, but casting to the left and right tends to bring individuals together. Even when an animal runs off some distance it nearly always swings back sharply and casts about until it regains contact with another individual or group. In spite of cutting back and forth, the momentum of the leaps quickly establishes a general direction of flight and, in this way, subgroups may diverge at first. Nonetheless, the tendency to cast about seems to encourage a rapid regroupment and the impala may settle down again as a single herd or split into several groups up to a kilometre from the site of their original scare.

Contact between subgroups and individuals is re-established without a sound and often in fairly thick bush, where the high jumps of their fellows are easily lost sight of. I consider it very likely that the peculiar leaping behaviour of the impala is correlated with the fetlock glands. As the legs make their "empty kicks" the fetlock glands give the appearance of expanding and they probably send puffs of scent up into the air, making scent trails which can be picked up by rapidly running animals without their having to lower their heads to the ground (as they do when following conspecifics at a walking pace).

Casting about from left to right may allow an animal to search for both visual and olfactory clues, but I suspect that the latter are most important, as jumping is commoner in bushland than in open country. It is interesting that impala, like some other antelopes, become excitable in a high wind; this is particularly noticeable before a storm, at which time there is much



"Empty kicking", from cine-film.

apparently spontaneous leaping and chasing about in what seem to be mock scares. Strong winds would presumably affect the impala's ability to regroup adversely, as olfactory signals would be very rapidly dispersed.

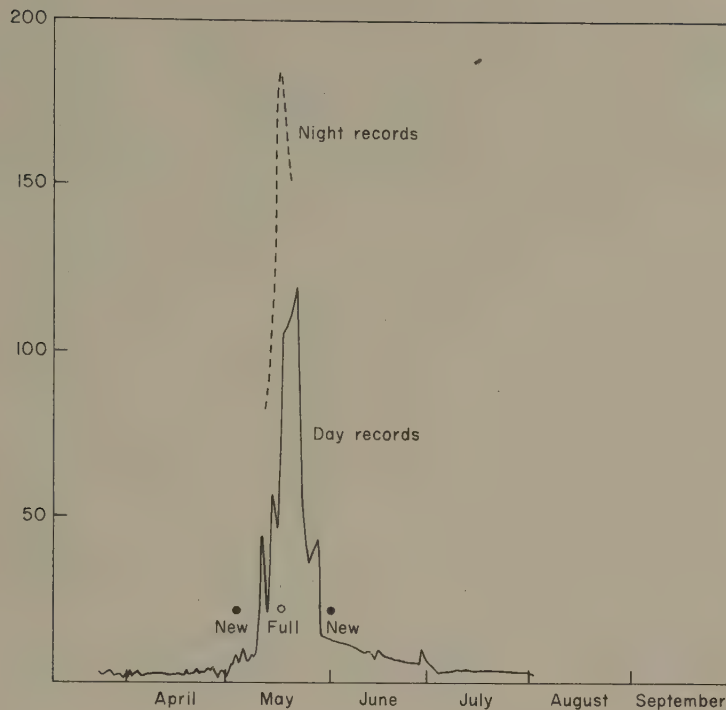
Jumping and empty kicking often appear to be simply expressions of excitement. I have seen a fighting male throw his fetlocks up into the air while on his knees; playing youngsters often alternate stotting with the rocking style of jumping and sometimes juvenile playing seems to stimulate some adult females into a bout of jumping. Schenkel (1966a) has described running zebras and gazelles also releasing this behaviour in neighbouring impala.

In male herds such behaviour may be associated with roaring, which led Leuthold (1970b) to suggest that the latter was simply a sign of excitement. I consider that the evolution of this extraordinary acoustic signal and its associated anatomical modifications has provided the solution to a problem posed by high densities and breakdown of the territorial system.

Schenkel (1966a) has described some of the situations in which roaring can be heard. For example, a dominant male distracted from his female herd by a rival may lose them in dense undergrowth. Schenkel saw a male roaring as he ran through dense bush at the gallop, upon which females came jumping out of the thicket from all sides and joined in normal herd formation. He sometimes saw a single adult male roaring repeatedly and on one occasion several females of a large herd nearby left their herd and its dominant male to join the roaring lone male. The male immediately started herding and courting, repeating his roaring display again and again. Schenkel also saw some bachelors take advantage of a fight to invade a herd, roaring and chasing the females. He considered that roaring induced bunching in the females and served to intimidate subordinate males and challenge rivals.

In areas with a short, intense rut, roaring is only heard at that time and Warren (1974) recorded as many as 180 roars in one hour. Leuthold (1970b) recorded roaring after fights and copulations as well as during chases. The roar would seem to derive from a bleating grunt made by most antelope males when they pursue a rival and are about to make contact. This signal generally elicits an extra effort to escape. The paradox that females are attracted to roaring males may explain a major function of the roar. A territory is an elaborate mechanism providing an undisturbed zone where a male can isolate and patiently break down an oestrous female's tendency to flee; for the oestrous female it is a refuge, for she can neither achieve conception, find time to eat, nor can she tolerate the stress if pursued by large numbers of males.

Where high densities of males and a seasonal rut negate this primary function for territories, females can mitigate persecution by clustering in



Frequency of roaring displays at Sengwa, Zimbabwe (from Warren, 1974).

large groups, and it is disturbance from males that is the most regular and pressing incentive for female crowding (not predators, as is sometimes asserted). Even so females, particularly those in oestrus, cannot escape the attentions of males. Roars determine their choice of consort because this signal indicates that other males will be absent from a comfortable zone around the roarer. This may explain why female impala tolerate fast, noisy males that would scare off other female antelopes and why "courtship" is abrupt and unritualized. It may be the principal reason why the borderline between dominance displays and courtship is poorly defined, a point well stressed by Monfort *et al.* (1973). This point is particularly relevant in relation to tongue-flashing, an apparently aggressive display that is often, but not always, associated with roaring and highly stereotyped in the impala. Schenkel called this gesture "empty licking" or "yawning" and he has interpreted it as a displacement movement in situations of conflicting tendencies. In fact, it seems to be intimidating when directed at a subordinate and has three important functions in impala society. Dominant males flash their tongue while approaching females and bachelors. Females tend to bunch in response to this signal while bachelors flee. In the case of matched opponents, one animal may stand and, raising his head, open his mouth widely, extruding the tongue several times in quick succession. This sign either precipitates flight or fighting; in either event it serves as a decisive element in the challenge. This gesture is also seen occasionally in solitary males when they indulge in bush-thrashing.

The origins of this extraordinary display are less likely to be displaced chewing, licking or yawning, than urine sampling. This ostensibly sexual behaviour might have acquired a ritualized aggressive connotation because



of the dominant males' very rapid oscillation between sampling females and pursuing rivals during both of which activities he roars and tongue-flashes. When a dominant male is bothered by numerous bachelors or challengers, the alternation of chasing and symbolic urine sampling becomes very rapid. It is even conceivable that tongue-flashing could intimidate subordinate males because of its close association with the juvenile experience of being herded by a dominant male. Since the tongue-flashing male is signalling his excited and actively dominant condition, the gesture is effectively both a challenge and a very economic way of testing an opponent, since only a self-assured male will not be intimidated. It is not only economic, but also specific and inconspicuous to other animals, so much so that few observers have commented on it. Tongue-flashing can also be seen as one of the manifestations of "speeding-up" in the impala's behavioural repertoire. All of these peculiarities of the impala are ultimately referable to the species' evolutionary history and its enigmatic exploitation of the habitat. Harrison (1936) noting their need for a combination of open space and shelter observed that impala at Shinyanga moved out of short-grassed parkland and into thick bush during the dry season and he interpreted the move as a response to food resources. There is, however, no universal correlation between seasonal movements and vegetation; the rut, shade and water needs may be other major influences.

Vesey-FitzGerald (1960) pointed out that impala on the floor of the Rukwa Valley are forced to congregate near waterholes during the height of the dry season but return to acacia country as soon as the first showers fall, restricting themselves during the height of the rains to islands of well-drained soil. Schenkel (1966a) also regarded well-drained but not precipitous ground, availability of water and a mosaic of wooded grassland communities as basic characteristics of the impala's habitat. Harrison (1936) noted how the diversity of plants around hardpans attracted many groups of impala but, with the growth of long grass and dense bush, they turned to short grass glades and the margins of the bush.

In many parts of East Africa impala emerge into open country at night and many observers have ascribed this trait to avoidance of predators. Yet during the overcast conditions of the wet season they can remain in the open all day, which suggests that the tendency to emerge on to grassland at night might be primarily influenced by avoidance of heat.

Using radio-tracking methods on a Kenya population close to its northern limits, Ables and Ables (1968) showed that, in addition to two diurnal peaks, there was a single nocturnal peak of feeding activity at about midnight, after which the females rested while some of the males remained active. Jarman and Jarman (1973) made quantitative tables of activity broken down into classes of animals and seasons. There are three periods of two to four hours' rest and rumination, the first in the middle of the day, the second at dusk after an evening feeding peak and the third following the minor midnight feed. At dawn all animals feed but there may be a minor pause in the morning. The abrupt changes in activity at dawn and dusk are indicative that they are pre-eminently diurnal animals, but Warren (1974) recorded peak activity in rutting males during nights of the full moon.



Impala feed on many species of plants, choosing only the green shoots and younger leaves. Harrison (1936) listed some 30 species of plants eaten in Shinyanga, of a similar range to those eaten by giraffe and kudu but, in this area, he found less difference in the species' composition of their wet and dry season diets. Important dry season browse was *Abrus schimperi*, *Combretum* spp., *Grewia*, *Sansevieria* and *Lonchocarpus eriocalyx*. However, the local floral composition is immediately reflected in their diet. Stewart (1971) found differences in herds less than 2 km apart because of the local availability of food plants.

The ratio of grass to browse varies from season to season and place to place. On the Mara, Talbot (1962) estimated 56% grass to 44% dicotyledons. At Tarangire, Lamprey (1963) listed 92.5% grass with the rest herbs, leaves and seeds, and he remarked on the seedlings of *Acacia tortilis* never being found anywhere other than in the dung of impala.

In the Kenya Rift Valley, Stewart (1971) noted *Cynodon* grass comprised 62% of their dry season diet but 47% in the rains.

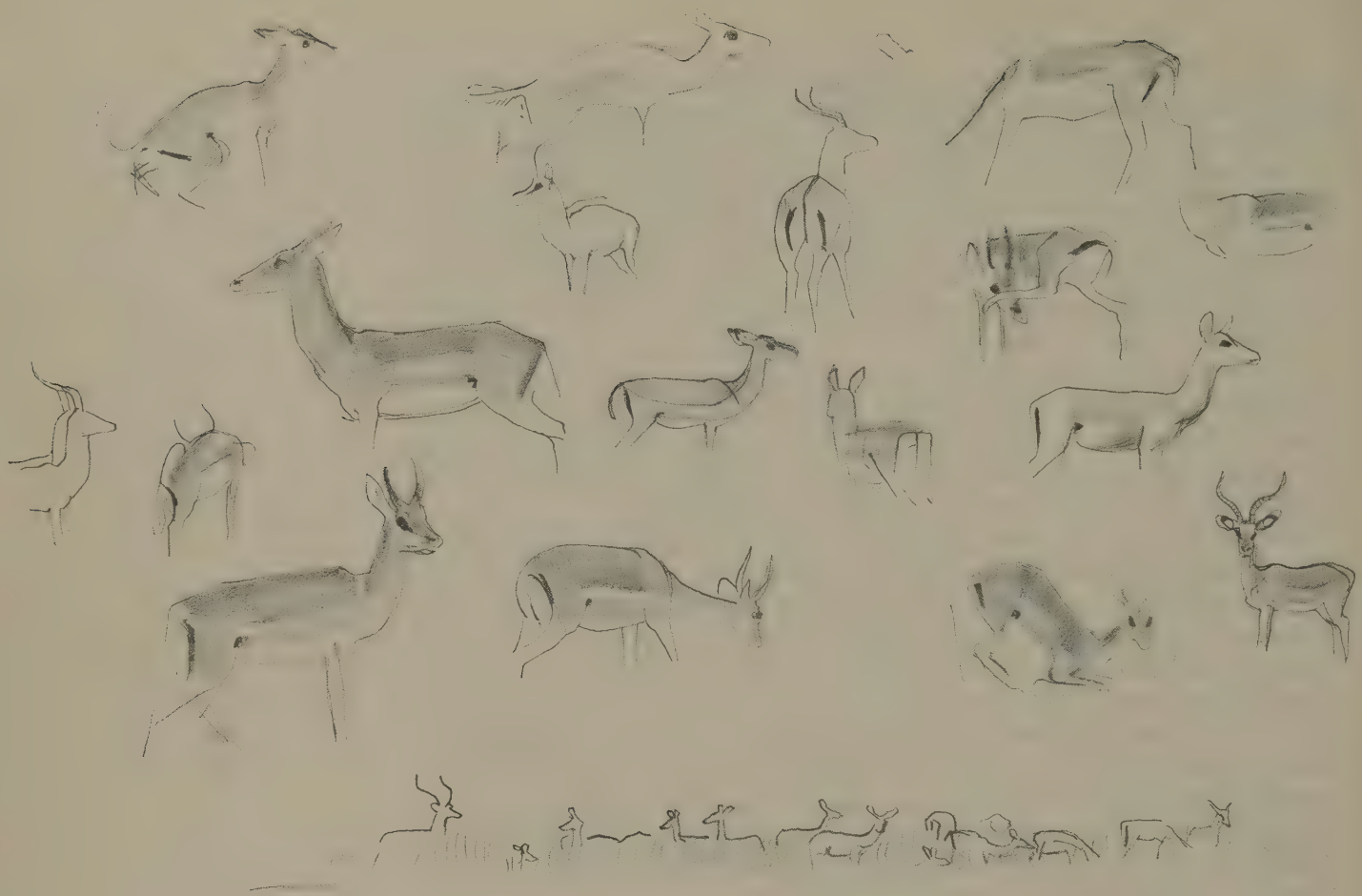
A catholic diet and something of the impala's evolutionary status are reflected in the structure of its digestive system. Likening the impala to some species of European deer in their adaptability to dietary extremes and tolerance of dense population levels, Hofmann (1973) noted that impala flourish on marginal lands where the vegetation is mixed and the animals' range is restricted. He found that the relief of the ruminal mucosa is intermediate between that of a more conservative ruminant and that of a grass-eating hartebeest or reedbuck. At the end of the dry season Hofmann found slender papillae in the ruminal atrium similar to those found in the last two genera. This feature is thought to be induced by a low protein, high fibre diet. The omasum resembles that of the reduncines and is more advanced than in gazelles.

Hofmann's perception of an overall resemblance with reduncines is interesting, as the impala may have made parallel but equivalent evolutionary progress into a grass-eating, water-dependent niche.

As the dry season progressed in Serengeti, Jarman and Jarman (1974) noted that groups of impala split up, spread out more widely and moved further every day in order to make use of the progressively more widely dispersed green shoots and leaves. Towards the end of the dry season, animals wandered more and more, travelling as much as 15 km from their wet season range.

Concentrations on flushes of new grass are widespread at this time of the year in all habitats. During drought in Rhodesia, Dasmann and Mossman (1962a) recorded exceptional journeys of 25 km to and from water and they remarked on the capacity of impala to move considerable distances in search of food, water and cover. When impala are forced to turn to drier, coarser and less nutritious fodder towards the end of the dry season, this leads to a rapid loss of condition and finally to malnutrition.

Impala mingle quite indiscriminately when attracted to a common resource. This is particularly noticeable at water holes or on isolated flushes of grass which may attract many hundreds of impala together with other grazing animals. In such transient concourses a social structure cannot be discerned. Leuthold (1970b) found that, although individuals kept frequent



company with others that shared the same range their associations were temporary for both males and females. The lack of individual attachments and the ability to form and reform into larger and smaller social units and range through several distinct vegetation zones emancipates the impala from limitations that severely curtail the activities of antelopes with more rigidly organized social systems.

Circumstances combine to inhibit any sustained relationship, but the need for them has also been lost at a phylogenetic level, even between a mother and her offspring. Jarman (1973) saw no signs of recognition between a mother and her six-month-old male offspring a few weeks after it had been evicted by an alpha male. Other pressures against sustained associations are inherent in opportunistic seasonal movements, fragmentation of female herds, the impermanence of a male's status and the general confusion that is characteristic of high density populations.

In some places, such as the Kagera National Park, Rwanda, impala sometimes number up to 500 animals per sq. km but habitat quality causes large variations in density. In this park Monfort *et al.* (1973) were able to correlate differences that they observed in the structure of impala society with the density gradient. Because contact and communication becomes more difficult in denser habitats and there is a natural tendency towards fragmentation in woodlands, these authors considered that this favours reproduction because it reduces the amount of interference and competition



between males. Noting the larger, mixed herds that aggregate in open areas with good visibility and the smaller harem and bachelor herds of the woodlands they emphasized a spatial and temporal separation of the impalas' activities.

At the lower densities isolated harem herds and bachelor herds were in evidence. At higher densities there was much competition by males in larger mixed herds to separate out groups of females. Because of the large numbers of animals around, only males of established dominance were able to maintain a small degree of physical isolation. This situation was considered by Monfort *et al.* to imperil reproductive success and act as a regulatory factor, but much more intense rutting is known in southern Africa and Fairall (1972) has pointed out that chasing, fighting and roaring might even help to trigger oestrus in the females. Certainly females can be observed being mated in many high density areas while they are concentrated on common feeding grounds.

Spinage (1973) has invoked photoperiodism to explain the change from a single short breeding season in southern Africa to the protracted bimodal pattern found in Kenya (Kayanja, 1969), but Skinner (1979) has pointed out that the male cycle in South Africa may be strongly influenced by a considerable loss in body condition during the short but very intense rut. So great are the physiological and behavioural changes that southern African males are incapable of breeding throughout the year (Skinner, 1971; Fairall, 1972; Skinner *et al.* 1974. The timing of the rut is enhanced by the great selective advantage of a birth season in the rains (Warren, 1974). Where ecological conditions maintain a large reservoir of well-fed males, as they do in Kenya, there are always other candidates to replace alpha males as they become exhausted, but the seasonal cycle in southern Africa brings all the males into peak condition at the same moment. In Sengwa, Warren (1974) found that one or two months before the May rut female groups commonly numbered over 150 animals and only 37% of the adult male groupings consisted of single animals. By May males had become intensely intolerant

of one another and 69% of the male groups were solitaries while female herds were fragmented, probably through a combination of male activity and the nature of the habitat. Most of the female groups were herded by a single male but over 10% of the herds were accompanied by up to six other males.

Loose all-male or bachelor groups are generally made up of "resting" adults and any young males showing a growth of horn. The latter are weeded out of the female herds during the rut.

At first the young males make persistent efforts to rejoin their mothers and, as there are generally several youngsters in this predicament, the fugitives tend to be together. They soon join groups of older males.

In populations with extended birth seasons there is a natural gradation by age in the size and weight of younger males and in the length of their growing horns. Within larger bachelor parties it is common to see a smaller animal approach a larger one with ears pointing forward and hindlegs tensed and ready for flight. Very cautiously it smells or nuzzles the other's forehead and eyes. The object of this inspection usually stands in a very erect symmetrical stance and submits to being sniffed without moving, his ears held well back and out of sight. Sniffs are occasionally followed by the passive but dominant impala allowing his neck to be licked but it may equally well be followed by a back-off or rapid withdrawal by the subordinate; occasionally there may be a sparring match but fighting is seldom prolonged or serious. It is possible that glandular secretions on the forehead, close to the margin of the eyes, convey information about the physiology of an individual and this in turn may influence the responses of other bachelors. The testing may help to avoid fighting and therefore sustain bachelor hierarchies.

Because of cycles in the biochemistry and reproductive physiology of the impala and because the animals are numerous there have been several studies. In East Africa, Kayanja (1969) has made a detailed description of the species' reproductive anatomy. In southern Africa, Anderson (1965), Skinner (1969) and Fairall (1972) have correlated the rutting period with increased weight in the males' reproductive organs and an increase in androgen secretions and spermatogenesis, which decline sharply after the rut. The external characteristics of a rutting or dominant male are (reversible) thickening of the neck, blackening of the skin around the eyes and various behavioural patterns, including exceptional activity, alertness and deliberate "proud" posturing. This self-advertising often takes place on dung-scattered stamping grounds which are used again year after year. Jarman (1973) reported a high level of aggression coinciding with a large-scale return by most of her Serengeti study population from their dry-season grazing to traditional wet season stamping grounds, and competition was particularly intense during the first weeks. Once males had established themselves in an area, they kept well apart and placed themselves between herds of females and the nearest neighbour.

Well-matched rivals make lateral displays from a distance or approach one another with slow deliberate steps. About one metre apart they swing out to present their profiles to each other. They may horn the ground or roar before clashing horns in a fight. If neither male retreats during a confrontation, the final signal for a horn clash usually follows. One animal



swivels his eyeballs, showing the whites, or nods his head slightly. The swing of the head is exactly parried by the opponent and both sets of horns tend to clash symmetrically with the convex medial portions taking the impact while the terminal flare locks the clinch. The two then try to push and throw one another off balance by sudden twists in which the head may turn through over 100 degrees. If the horns are not matched, one animal may get a horn through to the opponent's neck or shoulder. In this region adult males have exceptionally thick skin, an essential protection against the sharp jabs. When males do get killed in fights the wounds occur in the thorax or abdomen, where the skin is less thick.

Impala are taken by a variety of predators, lions, hyaenas, leopards, wild dogs and cheetahs being the most important. In the Kruger Park, where they are the most numerous of all ungulates, records showed that leopards killed more animals relative to their percentage abundance and lions less (Pienaar, 1963). A much higher proportion of solitary animals are killed.

Harrison (1936) saw many kills by leopards, cheetahs and wild dogs in fairly dense bush. He remarked that males gave the alarm during the rut whereas the females were more likely to do so at other times.

While aggregation into herds and group alertness may reduce an individual's susceptibility to attack, impala will nonetheless watch a predator kill one of their number without reacting very strongly, and Harrison (1936) pointed out that impala in the open did not scatter unduly when wild dogs

singled out an individual and followed it into the thickets. Their vulnerability to wild dogs and cheetahs is increased by the tendency to cast about from side to side.

Stephenson (1955) saw an adult impala leap twice into a pool with three hippos in it in order to evade a single wild dog. In southern Africa, a most extraordinary incident was seen and photographed at a pool, when a female impala was seized by a crocodile, which was in turn attacked by a hippo, which then tended the dying impala in a manner that suggested maternal behaviour. Juveniles are killed by jackals and the smaller cats, baboons, eagles and pythons. The mortality of newly born impala, particularly from predators, is thought to be very high and as most young are born very early in the wet season, before there is an abundance of thick grass cover, this factor is clearly not decisive in determining the reproductive cycle in this species. In equatorial areas there is a continuous breeding with two birth peaks in about March and November. In southern Tanzania and in south-central Africa most young tend to be born in November and December. The mating peak in these latitudes occurs in May and June. In Serengeti, Jarman and Jarman (1974) found the majority of conceptions occurred in March and April in spite of the fact that males had spaced out and started fighting with the first rains, the greatest number of females were in oestrus at the time when prime-age males were dominating the preferred feeding areas of the females.

It is significant that both sexes should be in peak condition at this time, having had the benefit of several wet months. The calves also benefit from their mothers' lactation during the rains and they are well grown and weaned before the main dry season.

The courtship behaviour of the impala has been described in detail by Schenkel (1966a). Once the male has tested and identified an oestrous female there is much chasing. Repeated flashings of his tongue seem to frighten her at first but the male follows her, his head lowered and sometimes grunting and bleating but not roaring. Eventually the female allows a closer approach and the male may lick her genitalia and he may rise and take several paces on his hindlegs. The display may be performed with erect penis. Schenkel saw dominant males walking on two legs while in a state of excitement after threatening competitors. The male made a mock mounting while still a few metres away from the female, this was shortly followed by actual copulation, after which there was sometimes an outburst of roaring and chasing.

Gestation is approximately six-and-a-half months and the young are normally born in a secluded spot, after which the calf remains lying out in some dense vegetation. The mother remains nearby and visits the calf to suckle it. After some days the young one begins to follow the mother but seeks shelter at the least alarm. Females with young stay close to thickets and bush. The mother communicates with a grunt and the young bleats in response to the mother or in distress. As many young are born at much the same time, it is easy for them to associate. Also the nursery herd may be restricted by the males at this time, so the formation can be quite tight. The young feed, rest and play together for much of the time but rejoin their mothers when on the move and stay close if there is an alarm. Their

growth is extremely rapid and both sexes are independent at less than one year, males are physiologically fertile from the age of 13 months and females conceive at 18 months.

Impala are numerous on many cattle ranches and are commonly cropped for their meat and hides.



**Hirola,
Hunter's
Hartebeest
(Beatragus
hunteri)**

Family

Bovidae

Order

Artiodactyla

Local names

Blanketta (Galla), Aroli (Somali).

Measurements

head and body

120—200 cm

height

100—125 cm

tail

30—45 cm

weight

80 kg approx.

horns

55—72 cm



Hirola, Hunter's Hartebeest (*Beatragus hunteri*)

The most distinctive features of the hirola are its long lyrate horns and its white-haired ears and tail. It also has white "spectacles" which serve to draw attention to the region of the forehead. Uniform sandy colouring may give way to slaty grey in the older males. A peculiarity of the males is the very thick skin on the nape, which folds up behind the horns when the ears are pricked. This ridge is not exceptionally fatty, nor is it an indicator of condition as Dracopoli (1914) suggested. It is simply an accommodation by the tough inflexible skin to a demand for movement in the ears, which are important signalling devices as well as sound funnels.

The horns arch outwards from a very short pedicel above the orbits but the backward turn is angular and in males this ramming zone is thick and heavily annulated. Compared with the open sweep of the impala's horns with which there is some resemblance, the long tips appear constricted because the shafts tend to run back and then up in parallel after the initial flare. The narrower span may be due to there being less emphasis on parrying an agile opponent and more on accurate ramming with the basal section. I have not seen *Beatragus* fighting but they are said to fight on their knees if fighting in earnest and wrestle with the horns in a standing position when lightly sparring.

The hirola poses some evolutionary and taxonomic problems. A larger fossil species, *Beatragus antiquus*, was described by Leakey (1965) from the lower Pleistocene at Olduvai, where it is known from Beds I and II. The same species has also turned up in somewhat earlier deposits at Omo and this animal was probably an ancestral chronospecies of the living hirola. Fossil fragments from Elandsfontein in South Africa may also belong to this species (Gentry, 1974).

In the fossil record *Beatragus antiquus* is found together with at least one smaller species of *Damaliscus* and another genus of alcelaphine, *Parmularius altidens*, which is a widespread and common species in Pleistocene deposits. According to Gentry (1974) *Parmularius* stock could be close to the common ancestry of both *Alcelaphus* and *Damaliscus* while the *Beatragus* line might even antedate this.

It is interesting that *Beatragus antiquus* occur in deposits together with fossils of small *Damaliscus* species and it is clear that the topi occupies a distinct niche and is not an incompatible species. Walther's (in Grzimek, 1972) lumping of hirola as a subspecies of *Damaliscus lunatus* is, of course, quite unacceptable.

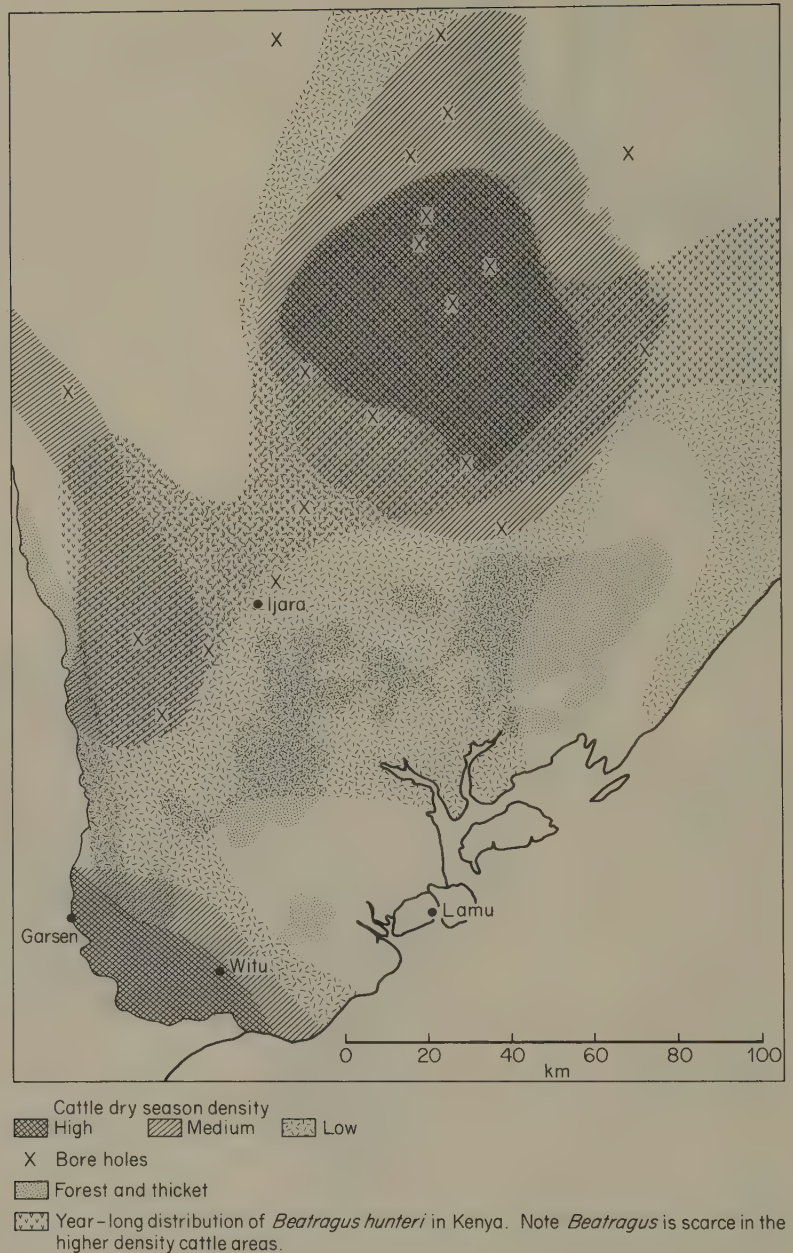
The hirola has not been studied in any detail but there is no evidence to suggest that it has unusual ecological requirements or that it exhibits a highly specialized behaviour. On the contrary, it is probably more generalized than either *Damaliscus* or *Alcelaphus* and it can be suggested with some confidence that it represents the last relic population of a formerly widely spread type. The absence of the true hartebeest (which is a very







Provision of bore holes allows cattle to expand and compress remaining population of *Beatragus hunteri* (now only common in 20 km belt north of Ijara). (Data from personal ground survey, Duncan, 1974; Dirschl *et al.*, 1978.)



recently evolved genus) from the hirola's stronghold may be the reason for its continued existence. On the basis of its feeding habits the hartebeest is certainly the most likely ecological competitor and it would conform with the general evolutionary pattern in which the end-product of a particular line tends to replace its immediate precursors.

On the basis of aerial and ground surveys in 1973 Duncan (1974) estimated that there was a total of about 10,000 hirolas in the Kenya part of their range, which was shared by about 200,000 cattle at that time. An aerial survey of a somewhat more extensive area was made in 1978 (Dirschl *et al.*, 1978). In the latter census 2,385 hirola were estimated and 454,414 cattle in the same census region. The discrepancy was partly due to the

larger area covered and perhaps partly due to different statistical and sampling techniques but the overall trend was unambiguous and ominous. They are found as far as Rama Addei in the Somali Republic but the largest concentration is in the low-lying Ngangerabeli Plain. Their habitat is a narrow strip of grassy plains sandwiched between the waterless acacia bush of the hinterland and the forest savanna mosaic of the coast. It is probably the subdesert to the north and the Tana River to the south that have kept other hartebeest populations out of this pocket of fine rangeland.

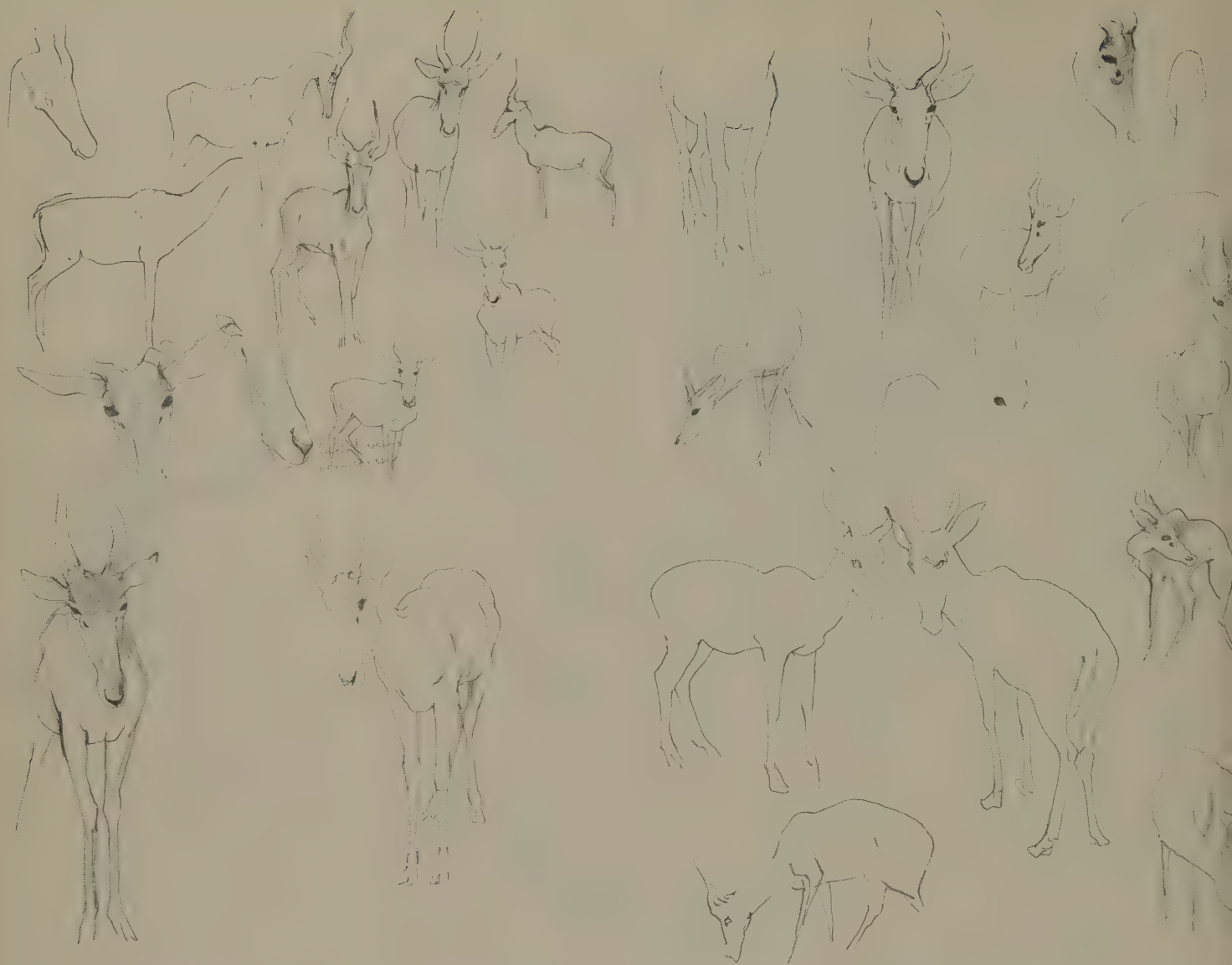
Brown (1965) had already reported that the range of this species was contracting. There was no evidence that this had been due to hunting, predation or disease but rather it is likely to have been caused by increasing competition for grass from large numbers of cattle in its habitat. The maps show how the main stronghold of the species is not only sandwiched between semi-desert and the coastal forests but also between two dense cattle populations.

Because pastoralists and their stock are dependent on water they have been unable to maintain themselves on dry plains during the hot season so the large herds of cattle are concentrated at this time around waterholes (mostly in the north-east) and along the banks of the Tana River. Traditionally, buffaloes suffered similar constraints. This has released pressure on the range at a time when grass is not growing and is a finite resource. The hirola has been able to monopolize a relatively large dry season range, which it shares only with common zebra, with oryx along the northern edges and with topi in the south. Even so, the present reduced range might be suboptimal even for the hirola and it could be significant that the animals captured in a large-scale capture experiment were found to be exceptionally delicate and subject to muscular dystrophy. If boreholes or irrigation were to open up the entire area to year-round grazing by cattle, the hirola's numbers can be predicted to suffer a further and possibly final decline.

The northern margins of the hirola's range coincide with acacia scrub where the grass cover becomes sparser. It may be this factor that limits the species rather than aridity alone, for the animals' relatively sedentary habits may reinforce their reliance on year-long and abundant grazing. It is capable of surviving without water but it seeks to rest or shade itself during the heat of the day. The quality of the grass is less important than the quantity and I found that both dung and stomach contents contained a high proportion of stems as well as dry sheaths and grass leaf. They are strictly grazers and they feed on dominant grasses of the region, notably *Chloris myriostachya*, *Cenchrus ciliaris* and *Digitaria*. Some of these are very coarse grasses and the rather large molars are well adapted to chewing such material. Feeding is most intense in the early mornings and evenings.

Females with young form groups which number between five and forty. These are often attended by a single territorial male but the nature and relative permanence of the association has not been ascertained. All-male groups are common and these occasionally associate with topi bachelors. Herds are thought to be relatively sedentary and solitary males particularly so. These territorial males posture on stamping grounds, which they scrape with the feet and mark with dung deposits. They have also been seen to insert grass stems in their facial glands and weave their heads.





Territorial and sexual behaviour possibly resembles that of *Alcelaphus* but no detailed study has been made. There is a seasonal breeding peak with most calves noted at the beginning of the short rains in October and November. The mating peak would therefore occur at the start of the long rains in about March or April (assuming a six to seven month gestation period). This timing accords with the predicted fluctuations in the adults' nutritional condition and the need for optimum grazing for growing young.

Like other alcelaphines the calves pass through a brief lying-up phase before they accompany the mother into a nursery herd and they are likely to be very vulnerable at this stage.

Lions are known predators of adults and hyaenas and cheetahs can also be expected to kill them while lesser predators may take the young.

The special importance and interest of the hirola lies in the context of bovid evolution and in our study of the progressive refinement of ungulates in exploiting grasslands. If we are to understand the important alcelaphine radiation the more generalized morphology and possibly near-ancestral position of this rare relic species must suggest many lines of enquiry.

Two attempts at a serious field study of the hirola have been foiled by the political situation in this remote borderland. Since 1965 this region has been the scene of much military activity and while it is difficult to guess how this has affected the status of the population it has certainly precluded the keeping of records, let alone any detailed study.

If the current plans for agricultural and pastoral development in this region are realized, an already contracted range will be constricted still further and at the expense of the better land. Stable development might possibly allow much more intensive conservation and protection but the species' survival can only become more hazardous as its range and numbers diminish in an insecure region.

A high priority should be given to further efforts at studying the animal in the field and there seems to be a good case for encouraging the build-up of breeding stock in parks and zoos elsewhere, particularly if this is allied with more intensive study of their physiology and a careful comparison of their biology with that of more successful species.





**Topi, Tiang,
Damalisc,
Bastard
Hartebeest
(*Damaliscus
lunatus*)**

Family

Bovidae

Order

Artiodactyla

Local names

Nyamera (Kiswahili), Topi (Kiamu), Jimela (Kinyamwezi), Tiang, Pura, Tengo (Lwo), Mangaazi (Luganda), Enyemera (Runyankole), Mukiyo (Nandi), Mumwe (Lusangu), Korke (Kiliangulu), Emuget (Karamojong), Amugete (Ateso).

Measurements

head and body

170 (150—190) cm

height

124 (108—134) cm

tail

43 (36—42) cm

weight

142 (120—155) kg males

130 (100—150) kg females

horns

35—60 cm

Topi, Tiang, Damalisc, Bastard Hartebeest (*Damaliscus lunatus*)

Races

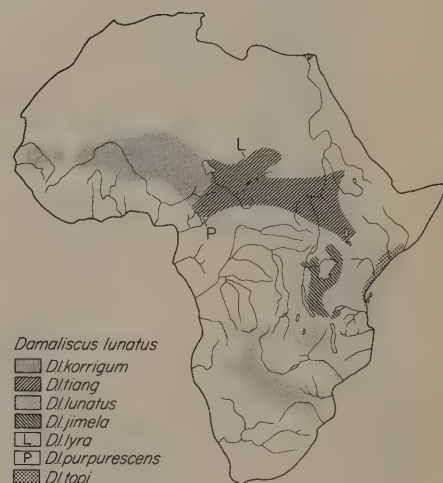
<i>Damaliscus lunatus topi</i>	Kenya Coast
<i>Damaliscus lunatus jimela</i>	Uganda, Tanzania, West Kenya
<i>Damaliscus lunatus tiang</i>	North Turkana (vagrant in Kidepo)

The topi, *Damaliscus lunatus*, has a bold pattern of black patches against mahogany brown with fawn underparts and legs. The coat is short and glossy with a sheen that alters the visual effect of the pattern according to how the light falls upon it. The possible role of pattern in the species' social semaphore has been discussed earlier, also the peculiar structure of the flat, heart-shaped nose was noted and illustrated (p. 458).

The distribution of *Damaliscus lunatus* is naturally discontinuous: there are also numerous areas where it has been displaced by man or his stock. The species is differentiated into at least five distinct sub-species. *D. l. lunatus* inhabits grassland between the Kalahari Desert and the southern woodlands with numerous small pockets within the woodland belt. *D. l. jimela* was once widespread in the Lake Victoria basin with outlying extensions to the south and west, while an easterly wing once ranged up to 2,400 m on the grassy uplands of the Mau. *D. l. topi* occupies a narrow strip of country between the coastal forests and the Somali arid wedge. *D. l. tiang* has the most extensive range, from the middle reaches of the Nile Valley to Lake Chad—while *D. l. korrigum* originally ranged over much of the flat open country between the Sahara and the West African forests and woodlands.

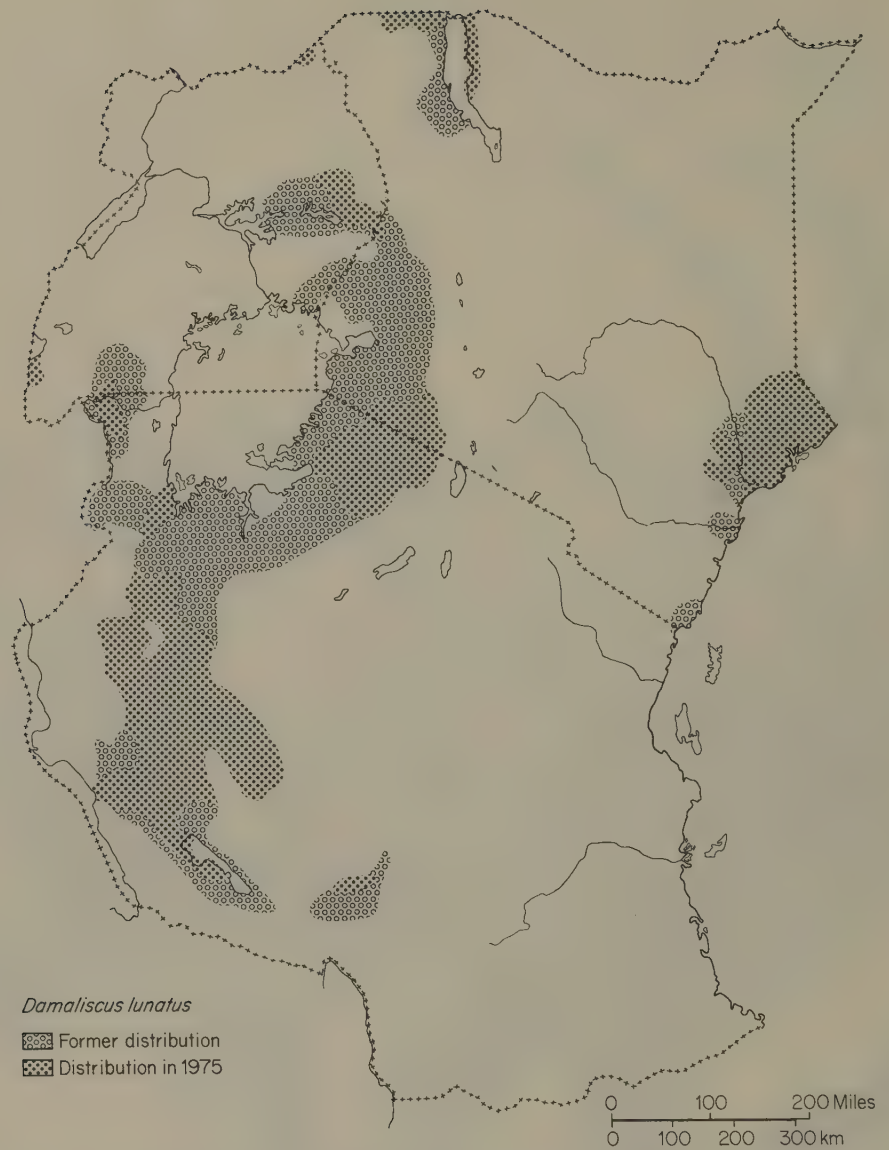
This species also tends to be relatively abundant in an area or totally absent. Scattered individuals do not occupy a locality for very long—with the passage of time they either die or multiply. Possibly their fragmented distribution has been influenced by the species' reliance on population nuclei (whence they can expand if conditions are favourable). Throughout its range *Damaliscus lunatus* exploit sump areas or flood plains for the green grass that is their essential requirement, and it is significant that it was observation of topi in the Rukwa Valley that led Vesey-FitzGerald to his pioneer studies of grazing succession and the roles of the catena in seasonal feeding patterns and of ungulate herds in conditioning and improving the range by massive trampling and cropping (see Vesey-FitzGerald, 1955a, 1960, 1965, 1973a; and Vol. I, pp. 38—40).

The effects of both drought and floods are most marked in habitats such as Rukwa, and it may have been extremes of both that influenced the remarkable fluctuations in topi numbers that have been recorded from several localities. When there is inadequate green grass individual topi lose condition and fail to breed but they recover fast with access to fresh fodder

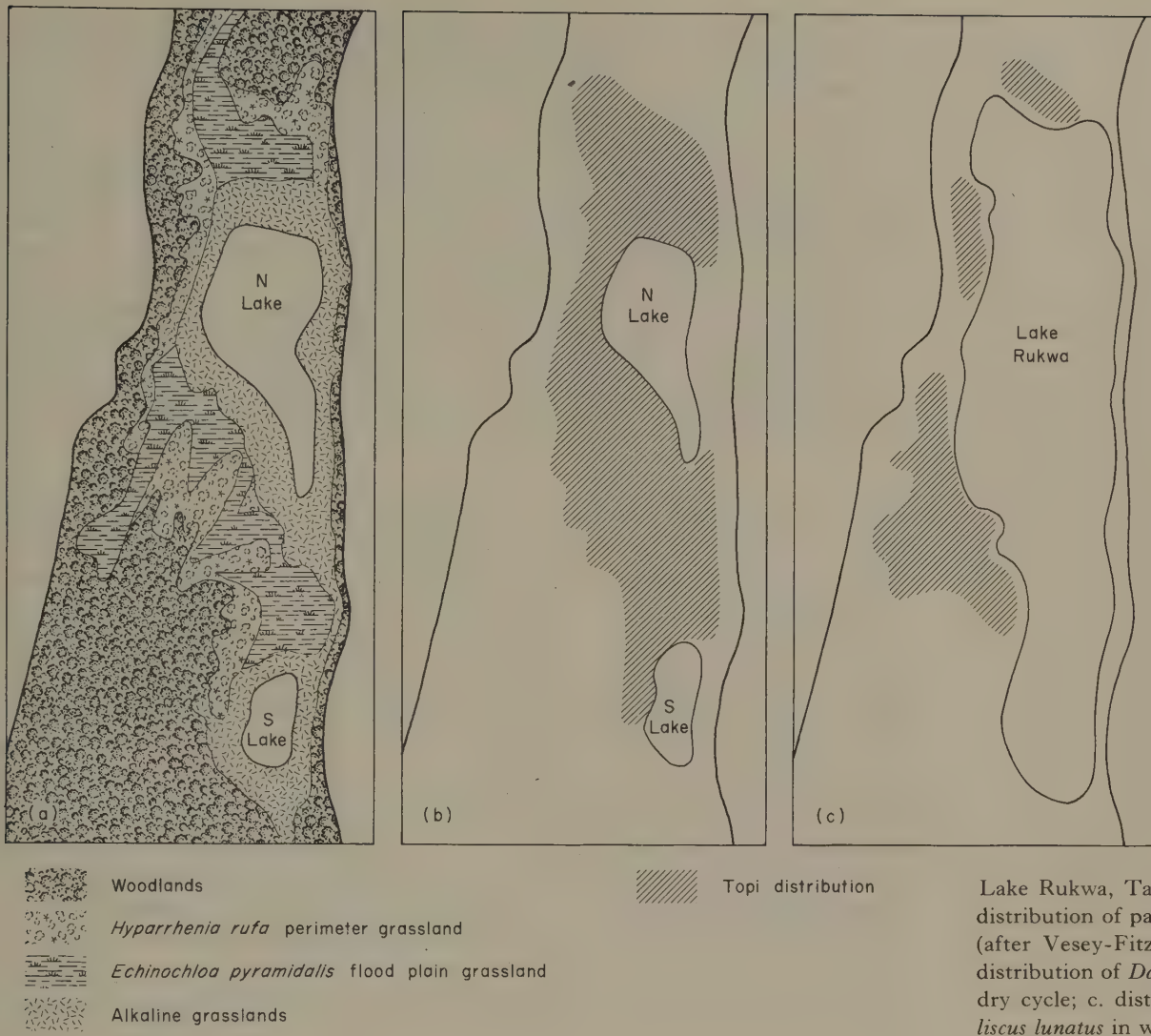








and their numbers recoup rapidly as the animals grow quickly, mature early and are fecund. Drought and flooding exert fundamentally different pressures on topi populations. If they have no green fodder over a long enough period their numbers decline rapidly; so severe and prolonged famine eliminates the topi from all their marginal habitats. Paradoxically, positive extension of range may occur on flood plains during drought because the topi is able to use most of the vegetation belts that follow the receding waters. (In this connexion the topi's name in the Jonglei area of the South Sudan is synonymous with a word for mud.) Vesey-FitzGerald (1955a) remarked that the Rukwa topi apparently suffered no inconvenience from the extended drought of 1949—1954. Indeed they exploit some of the littoral zones, particularly favouring alkaline pastures of *Sporobolus spicatus*, *Odyssea jaegeri*, *Vossia* and *Juncellus*, where they may graze in small parties. Furthermore, they can survive exposure to intense solar radiation without needing to drink. In other regions drought often contracts the total range of



Lake Rukwa, Tanzania showing: a. distribution of pastures in dry cycle (after Vesey-FitzGerald, 1965). b. distribution of *Damaliscus lunatus* in dry cycle; c. distribution of *Damaliscus lunatus* in wet cycle.

populations and limits them to green lacustrine or valley refuges. In Botswana Child *et al.* (1972) noted that *D. l. lunatus* became very thin after three-and-a-half months without water and were very reluctant to leave dense shade at this time. These authors thought that shade might be a critical factor in determining habitat in this area where these animals favour the abrupt fringes of grass and woodland. By contrast, heavy rains tend to concentrate portions of populations on small areas of higher ground where their large numbers or the presence of other ungulates helps keep the grass short and palatable through continuous grazing and trampling (Vesey-FitzGerald, 1955a). For relatively short periods concentration may be advantageous but between 1960 and 1964 the level of Lake Rukwa rose to the point where most of the topis' traditional grazing remained under water even during the dry season. Many deaths followed and there was virtually no breeding for two years. Yet the topi and to a lesser extent other species soon made a remarkable accommodation which has been described by Vesey-FitzGerald (1965).

"After the initial set-back caused by the rising water, during which time some small groups of animals were drowned and numbers of young died from cold, hunger and general debilitation, an adjustment to the prevailing circumstances became apparent. This was manifest by the production of a grazing mosaic in grasslands that were not formerly utilized, and of a restored grazing sequence and pasture rotation along the high-water mark of the flood in areas that were not formerly frequented. . . . The plains animals normally made no use of this rank herbage, but as an expedient for survival during the high floods great numbers concentrated there, thus initiating unusual grazing pressure and trampling down the rank herbage. . . . In the spaces between clumps of the tall species of perennial grass, which were no longer shaded by top growth, caespitose (*Cynodon*, *Chloris*, *Brachiaria*) species of grasses grew more vigorously than usual as a result of utilization. . . . In a surprisingly short time (second season of occupation) the landscape changed from a fire-dominated one to one modified by grazing, and the evacuee herds showed signs of improvement in condition."

This situation not only illustrates the dynamic role of ungulates in conditioning their range and food supply but also shows how topi can quickly adapt to very harsh seasonal contrasts without relinquishing their dependence on green grass. Such climatic oscillations are widespread over the grassland and savannas that lie wedged in between the hot African deserts and the moist woodlands and forests. Huge areas that are unfit for grazing during one season or cycle offer abundant resources during another, and it is the broad outlines of these cycles that are evident in the Rukwa Valley (see p. 489). The climatic extremes of this area have provided a model of the topi's environment and have suggested something of the animal's ecological specialization. Elsewhere *D. lunatus* may live in a still harsher environment, as it does in Botswana, where Child *et al.* (1972) have described *D. l. lunatus* living on the margins both of its geographic range and of its physiological tolerance; or it may inhabit more benign habitats, as in south-western Uganda.

This species has been the subject of several intensive studies (Child *et al.*, 1972; Joubert, 1972a; Jewell, 1972; Duncan, 1975; Monfort-Braham, 1975) and the picture of a remarkably flexible social organization has emerged. It is clear that the spatial and seasonal distribution of edible green grass through the habitat is a major determinant of the species' movements and social groupings. Duncan (1975) found that Serengeti topi apparently attempted, by selective grazing, to maintain high ratios of grass leaf in their diet during both seasons. Although they eat most grass species, at any one time they may be strongly selective, very often for grasses with the longest leaves. Field (1972b) found that miniature grasses and dicotyledons were absent in the diet of topi at Ishasha but in areas where the dicotyledons are abundant in the sward they are eaten, though in small quantities. The ground-hugging miniature grasses are probably avoided because they are more difficult to crop and it is impossible to differentiate between the tiny leaves and stems, a discrimination that is achieved by a grazing topi on the basis of differences in the breaking points when pulled. Duncan recorded topi moving out of areas that had been invaded by gnu and suggested that they were unable to crop the ground as closely as the gnu. Examining the differences between topi from two areas of the Serengeti Park, Duncan

found that one population, like the Rukwa topi, moves in large herds at the end of the rains from the upper end of the catena to the lower end. Here the plains are open and rolling but where the landscape is more dissected very small groups of topi are resident because their year-long needs can be met within a small area. In these localities the adult males are spaced out in territories which they share with well-established females. Joubert (1972a) studying *D. l. lunatus* in a woodland habitat in southern Africa also found territorial males with exclusive female groups but the animals were often widely dispersed and single bulls defended areas of 2—4 sq. km.

Female topi are aggressive and hierarchical but in woodland territories Duncan found them reinforcing the exclusiveness of their shared territory by threatening, chasing off or even fighting intruding females or yearlings. He even saw them display herding behaviour that is normally the means for a male to detain females within the territory; in the case of females it was to force intruders to bunch and drive them out. Given the finite resources of a residential herd's home range, such exclusion of other topi by both sexes has the function of conserving resources and maintaining an ecological equilibrium with the home range. Duncan recorded individual females occupying the same territory throughout his three-and-a-half years study period, which implies a remarkable stability and a more or less closed membership of female groups. However, the boundaries of territories probably acquire their significance for females through the repeated herding activity of males, and no female makes the ritualized boundary displays that so preoccupy the males. A very similar situation was found in the southern part of the Akagera National Park by Monfort-Braham (1975) where the topi lived in scattered groups of ten to twenty individuals on territories of 25—50 ha; at the time of her study topi represented about 3% of large herbivore biomass (buffalo being the dominant species). Over the three or four years of Monfort-Braham's observations known females and territorial males remained within limited areas and she suggested that the females' attachment is probably life-long, but she considered that the relative stability of group membership was strongly influenced by the frequency of encounters with other females.

This situation is contrasted with that at the north end of the park where the hills and valleys are broader, less dissected and there are large areas of seasonal grazing. Here topi represented 56% of the total herbivore biomass at a mean annual density of about 36 topi per sq. km. Seasonal pastures were about 30 km apart but Monfort found that marked topi in this area retained an equally strong attachment to a locality in spite of their movements being more extensive and the area therefore being very much larger. Valley floors were the sites for large gatherings in October/November. Territorial males were scattered about but the pastures were swept over by herds of up to 2,000 animals. Breeding was seasonal and Monfort-Braham observed that when the females in these herds started to come into oestrus they activated males which travelled with them in mixed or bachelor herds during the rest of the year. Up to 100 males would take up position on traditional grounds, where they were densely aggregated in temporary territories. Similar clusters of territories in other areas of high topi density have been recorded, in Rukwa by Vesey-FitzGerald (1955) and in Serengeti by



Duncan (1975). The size as well as the functional importance of these clusters is a direct measure of the size of parent herds, and as such can reflect the area of supporting pasture. Monfort-Braham found the largest clusters on the broadest plains and smaller ones in the narrower valleys. The larger the cluster the more constricted the size of individual territories with distances between males narrowing to as little as 25–40 m. Vesey-FitzGerald described similar “stamping grounds” in the Rukwa Valley where “each male has his patch of ground trampled bare, a little castle he can call his own where he daily deposits his dung, most of the chasing and mock battles seem to be connected with defending this little patch of sacred ground.” Such males are forced to leave daily and seek food and drink; once they are away they revert to bachelor status becoming quiescent and gregarious. Most of the animals within this cluster are in an almost permanent state of excitement, what with all the coming and going, the challenges and fights. All this tends to make the clusters very conspicuous and noisy centres of activity.

Monfort *et al.* (1973) recorded a restricted mating season between December and February in South Akagera but conceptions took place over at least four months in the high density areas in spite of the northern area having the same climate and vegetation composition. However, subsequent births were not evenly distributed but appeared in echelons. Monfort *et al.* explained this as the product of a local pattern of movement, whereby large population units containing a high proportion of females moved over extensive areas of their range with relatively few being inseminated by the isolated males through whose territories they passed. However, grazing being cyclic and rotational, with the valleys serving as funnels, mega-herds inevitably encountered the territorial clusters which were well placed in the path of their movements. While the herds lingered in the immediate vicinity of the territories there were numerous matings—hence the echelons of births eight months later.

What are the mechanisms behind the high proportion of conceptions achieved on territorial clusters? Monfort-Braham’s conclusion that it is the presence and sexual condition of a mass of females that first triggers the males’ annual re-occupation of territorial clusters implies a chain of inter-related hormonal changes which should be investigated. Why are fewer females inseminated in the intervals between visits to the territorial clusters? Is the exaggerated behaviour and loud vocalizing of densely aggregated males, in turn, the high-density substitute for a patient, prolonged courtship, serving to abbreviate preliminaries and induce receptivity in the female? Only a detailed monitoring of annual cycles and the close correlation of hormone levels with social and environmental stimuli is likely to give satisfactory answers.

Wherever there are large populations of nomadic *Damaliscus lunatus* it is observable that males relinquish their territories if no females visit them. This reinforcement is even more necessary for the males on territorial clusters whose tenure is temporary, whose origins are within a mega-herd and whose behaviour may have been precipitated in the first place by the females’ reproductive cycle. It would seem, therefore, that it is the predictability of female visits that determines whether territorial clusters are maintained.

Where pressure of numbers demands continuous movement in search of fresh pastures and there are no geographic features to guide the movements of mega-herds along predetermined paths, sedentary territorial males may be inadequately reinforced because of the unpredictability or length of time between herd visits. In these circumstances males that are rewarded are those that reconcile the spatial intolerance inherent in rutting with the need to keep up with the females' vagaries of movement. This seems to have been the situation reported by Jewell (1972) from Ishasha, where there are shorter biannual wet seasons, breeding continues throughout the year and the timing of mating peaks is very variable. Here topi are a dominant grazer in an ungulate community of very few species and this may influence their high density in this region (up to 50 per sq. km). The effect of this is that the herds move continuously thus rotating their pastures. The large numbers of topi quickly finish the grass and the mass of animals must keep moving so that males that have attached themselves to a piece of ground are soon deserted by the rest. In this situation it is probably the presence of many cows in oestrus and the challenge of other bulls that stimulates bulls to maintain their herding behaviour at the maximum intensity. Cows are herded and copulated with by a succession of males in the course of a single day and the whole mass of topi is divided up into units of females with young each tended by a bull, which Jewell (1972) called "wards". These might contain as many as 83 females and, because of the forward movement, the groups in the van are generally the largest. Jewell recorded an overall preponderance of females in this population of three to two males and a calf ratio between 24 and 62 per 100 females. Of all males 25% were judged to be infertile yearlings, whereas females of the same age were capable of breeding. In dense aggregations the bulls become distracted by their herding and interactions with their neighbours are brief but, if excitement is intense during the rut, horn clashes between neighbouring males and copulations may alternate in quick succession and the whole herd appears to be a centre of feverish activity.

When the females are not claiming all the attention and the males are well spaced out in their territories the interactions between neighbours are generally rather leisurely and highly ritualized. These interactions take place in the course of visiting the boundaries of a territory or, in the case of small territories, in direct response to another male's activity. Observation of a neighbour is often conducted from a "stamping ground", patch of bare earth or from the eminence of a termitary. Military sportsmen and officials have invariably interpreted this as "sentry duty". Walther (in Grzimek, 1972) suggested they may be cooling their legs in a ground breeze, while Joubert (1972a) described it as static-optic marking. Females also exhibit this behaviour but Duncan (1975) never found them actively patrolling boundaries and their activity was more evenly spread throughout the home range.

The bare earth is pawed with the forefeet, which have interdigital glands. This presumably scents the scrape but as the rut may be at the height of the rains the tramping and scraping often creates a hard pan which fills with water, giving the impression that the scraping topi is playing at splashing. Several such scrapes are maintained by pawing and horning, and they are also marked by piles of the owner's dung, which are continuously added



to and on which the topi occasionally rests but never rolls. The deposition of dung and urine is accompanied by highly distinctive postures which also seem to attract the attention of neighbours (see opposite).

In the course of patrolling its home range the topi also deposits scent from its preorbital glands on to vegetation, even stripping the end off in order to insert a stem or twig into the gland. Subsequently the animal weaves

its lowered head and horns back and forth so that glandular scent collects in the annuli of the horns and the hair of the face. The stem may then be nibbled and the action repeated. Of all classes of topi territorial males have the largest, most active face glands. As with some of the neotragine antelopes, the depositing of secretion on to grass stems and its transference to the topi's face and horns is a delicately conducted operation; the side-to-side rubbing of the face and horns on the ground or on termitaries is a more vigorous gesture. Also as in neotragines, horning the ground may be a form of redirected threat or vacuum activity since it is most commonly seen in males after excitement such as chase, territorial encounter, fights or shepherding.

The most important advertisement and assertion of territory is the presence of the male topi himself. The habit of standing on termitaries not only makes him conspicuous but often sharpens the angle of the body to make a more emphatic vertical signal. In addition to this static posture the male also gallops around his territory or cavorts. This may be initiated by the presence of other males but occasionally it seems to be quite spontaneous and gives the impression of being playful.

All these forms of advertisement and territorial marking are employed at some time or other when the topi interacts with a neighbour. The interaction frequently appears to be invited, for a male will walk over to visit his neighbour, pausing as he does so to look from side to side with ears pricked forward and head well up.

At higher intensities an animal will throw its head up in the air and hold this position for a second or two just before jerking it down into the lowered threat position.

Ritualized flagging of the head may be returned by the neighbour as they come together; then both males stand side by side and smell one another's anal region. Both topi may keep very still, except for twitching the tail and some continued flagging or casting of the head. These preliminaries may then be followed by defaecation, pawing, cavorting, horning of the ground or flight by the inferior animal.

Joubert (1972a) described his observations of challenge rituals among *D. l. lunatus*.

"If one of the animals retreats and runs away the dominant male will usually give chase and attempt to gain a position ahead of the inferior male. Even while giving chase at speed the challenger keeps throwing up his head and once he has succeeded in passing the retreating male he will jump up into the air and simultaneously turn his flank to the other male (lateral presentation) and throw his head up. If this stops the fleeing animal, head casting between the two is again resumed . . . the more intensive the casting becomes the higher the animal attempts to lift his head until the demonstrator eventually rears up on his hind-legs. This obviously confers a higher degree of 'threat' value to the display and precedes actual fighting."

As I remarked earlier (p. 450) the markings of the topi may enhance the impression of height in this rearing display, as in the termitary posture. If a fight ensues both animals swing face to face, drop on their knees and, almost laying their foreheads against the ground, lunge forward and entangle their horns. Sometimes there are pushing duels which may last many minutes. It is rare for one of the adversaries to be wounded or killed. In

fact, the challenge rituals often pass off with no sign of a fight and after a bit of head flagging both participants graze their way away from their mutual boundary.

Only neighbouring territory holders participate in these challenge rituals and wandering bachelors generally run away from an approaching territorial male, whereupon they are chased.

Their gallop is fast with their head carried low but young animals and some adults sometimes keep the neck erect with chin tucked in, meanwhile bouncing along in a similar run to that used by the hartebeest. This gait tends to be adopted by smaller animals approached by a bigger topi or when they are mildly alarmed by humans or predators. This grotesque but very eye-catching bounce is probably directed in the first place at other topis and may derive from an erect juvenile posture put into motion and designed to inhibit attack. However, there is an opposite gait seen among juveniles that is clearly submissive and directed only at other topi, towards which the animal canters with its head close to the ground. This gait is more rarely seen, is inconspicuous and seems to be directed at another individual, whereas the bounce is non-directed, obvious and more commonly seen. What is striking is that both gaits seem to represent static postures set into motion.

Solitary topi are rather quiet but they snort loudly when alarmed and the males grunt as they try to herd their females or while mating. Females rumble or grunt gently at their young and the young bleat and even squeak in excitement.

The seasons alter the topis' activity cycles. During the dry season they tend to rest in the middle of the day standing or lying down in the shade. If they drink they tend to visit water in mid-morning or before dark. Duncan (1975) found that the time spent grazing was 40–45% of the 24 hours; this remained relatively constant and there appeared to be little variation in the quantities of food eaten. The males reduced their grazing time to 36% during the rut. He also found that the males were on the move three-quarters as much again as the females. In general, grazing is most intense at dawn and dusk and the animals are normally wholly diurnal and lie up during the night. It has been suggested that the topi's choice of nocturnal rest sites may be determined by a need to avoid predators and it has also been assumed that predation and poaching have been major influences on the population fluctuations that have been seen. Bourlière and Verschuren (1960) reported that a great increase in the number of topi on the Rutshuru–Rwindi plains followed the shooting of large numbers of lions at about the time of the first world war and this increase appeared to coincide with a decline in the numbers of Uganda kob. When this area became a national park in 1929 all species benefited initially and an estimate of populations made in 1930 gave 10,000 topi, 15,000 kob and 250 lions. Within ten years the topi were thought to have declined to 1,200 and the kob to 300 while hippo and buffalo increased. Subsequently topi were seen to increase during the forties and 4,800 were counted in 1959. Even allowing for considerable errors in estimation, the fluctuations were clearly on a remarkable scale. In the neighbouring Ishasha area fluctuations have also been observed and a total range of 80 sq. km was used by 3,800 topis (1 per 2.1 ha) in 1970 (Jewell, 1972).



Dissection of male *Damaliscus lunatus* head. Compare with figures on pp. 399, 439 and 445.

Topi are known to be the principal food of the lions in this area and hyaenas are also numerous but there has been no measure of their role in limiting the topi population. On the Rwana plain in the Serengeti Park, a habitat of about 80 sq. km, Duncan (1975) estimated that the population doubled in about two years from less than 2,000 to 4,000. In the Rukwa Valley the total population has certainly fluctuated by at least a third. Here the environmental factors contributing to a decline in numbers could be observed directly during the 1961–63 floods, when both the flood plain and the lakeshore grasslands were under water. Attempting to follow the traditional cycle, significant numbers of animals died after moving down into the flooded range. Moving back up the catena the topi invaded *Hyparrhenia* grass in open woodland. This species of grass grows taller than the topi and the sharp seeds are reported to have blinded many individuals as they tended to panic very easily in this dense and unfamiliar cover. Although grazing swards were eventually formed in normally unfrequented areas, there was considerable mortality at first from accidents and malnutrition and the population's decline was reinforced by a virtual cessation of breeding for two years (Balson, personal communication). Disease may play an important part at such time but large-scale die-offs from disease have not been reported for topi, although an epidemic of "blue tongue" affected the Ishasha population at one time.

Estimates of the ratio of young to adults have been made by numerous observers and very divergent percentages have emerged. The relative influences of seasonal breeding, female fecundity, disease and predation are difficult to assess but it is interesting that the smaller *Damaliscus dorcas* was shown to have suffered heavy predation from jackals before predators were controlled. Du Plessis (1972) reported that the survival rate of young blesbuck rose from 37%, before the number of jackals was reduced, to 85%

which is some indication of how vulnerable young *Damaliscus* are. There is a period of weeks during which they are vulnerable to most of the large carnivores. Kruuk (1975) has illustrated wild dogs killing a topi calf and being robbed of it by a hyaena.

Ecological limitations on topi are probably augmented by competition. The hartebeest is the commonest alcelaphine over large parts of eastern Africa (see p. 507) but, in the areas where both species overlap, the highly social topi normally outnumber the hartebeest. Nonetheless hartebeest are probably hardier and therefore superior in less favourable habitats. In western Serengeti, topi move when the gnu migrations arrive *en masse*. Duncan (1975) noted that the gnu eat a younger growth stage and, as they graze very closely, the large herds certainly pre-empt the resources for the period they invade the topi's favourite habitat. He has also guessed that large numbers of cattle and topi cannot co-exist on the same dry-season range and competition with cattle certainly explains the decline of the topi in some areas, where cattle populations have slowly built up to a high density. Child (1968) has concluded that decline in numbers of *D. l. lunatus* occurring in Botswana may have been due to deterioration of the habitat, bush having encroached on the perennial grasslands on which *Damaliscus* is dependent. In this deterioration he also suggested that competition from increasing herds of impala might be a constraint.

It has already been mentioned that breeding and territorial behaviour patterns are subject to much regional variation. Where the topi live throughout the year on high quality rangeland and during years of well-distributed rainfall there is generally some breeding going on all the year round. Where breeding is a markedly cyclic phenomenon as it is in Botswana, Child *et al.* (1972) have shown that there can be a good correlation between improving physical condition and increased testes weight, both of which were encouraged by the good grazing that was available in the preceding months. Figures also showed that the rut was followed by a very sharp decline in condition and testes weight, a phenomenon that is common in many rutting ungulates that feed less than usual and therefore fail to balance their greatly increased expenditure of energy on territorial behaviour. (However, this phenomenon does not apply to the alcelaphine gnu, see p. 531.) In Botswana and in Rukwa this decline is followed by a long dry season and a widespread dispersal of the herds, so both physiology and environment might help to inhibit further sexual behaviour for at least six months. Recovery from the after-effects of a rutting peak could be one of the factors influencing periodicity.

Child *et al.* also assessed the condition of females and noted a drop in their condition which coincides with the later stages of pregnancy and lactation.

Males follow oestrous females very persistently with their neck and ears lowered, the nose and tail erect, high stepping with great deliberation and the exhibition of this peculiar posture seems to be the most important element in courtship. If the female indicates receptiveness she stands with her tail raised. If the male approaches from the side he may occasionally jab up at her belly with the foreleg but close contacts and ritual are abbreviated and this is quickly followed by a very fast copulation. Bulls





mount an oestrous female repeatedly and, in large companies, she may be inseminated by several bulls in the course of a day. Gestation has been recorded as 235—241 days. At birth the calf weighs about 12 kg and is a uniform fawn colour. It is not able to run for some hours and is left hidden in long grass but, after a period that varies from a few days in the mobile Ishasha population to a week or two in Serengeti, it joins the mother and other females and young in a herd. The young often gather together spontaneously and the females tend to face out from this nucleus at the slightest alarm, so that a ring of adults surrounds the young. This formation can be seen in response to vehicles and apparently also to herding by a territorial male. Just before, and for some time after, giving birth females tend to avoid mixed herds and form small nursery groups.

At about three months of age their horns are showing and adult colouring appears. They have a highly characteristic pony-like posture when approached by adult males, with the tail raised and chin tucked in. Male calves are often chased by territorial bulls but female calves stay about until the next calf is born. The onset of sexual maturity appears to be influenced by the environment. Jewell and Duncan found pregnant yearlings, whereas Child *et al.* found the heifers first conceiving at over 28 months of age and males becoming sexually mature at 40—42 months. The Ishasha males mature at 30 months.

Such exceptional growth rates must contribute to the potential of this species for sustained-yield cropping.

In and around sump areas large and healthy populations of *Damaliscus lunatus* can often co-exist with cattle long after the areas practical carrying-capacity for livestock has been reached. In such areas, the nature of such ecological partitioning should be exactly documented with a view to increasing production and encouraging multiple land-use while maintaining a balanced ecosystem.



Alcelaphus buselaphus lelwel.



**Hartebeest,
Kongoni
(*Alcelaphus
buselaphus*)**

**Family
Order
Local names**

Bovidae
Artiodactyla

Kongoni (Kiswahili), Kundro (Madi),
Ngonde (Kikuyu, Kipare), Nkondi
(Kimeru), Lkonde (Samburu), Ol kondi
(Masai), Naondi (Kikamba), Ennangaazi
(Luganda), Endagazi (Runyoro), Mujia
(Kinyaturu), Isubhugyya (Kijita), Orobout

(Ndorobo), Ekereo, Etulia (Turkana),
Eloba (Karamojong), Laba (Bari), Pura
(Lwo), Nyangu (Kiliangulu), Sig (Somali),
Chepunyogoswet (Sebei), Degra el Ouach
(Arabic).

Hartebeest, Kongoni (*Alcelaphus buselaphus*)

Races*

Alcelaphus buselaphus lelwel

Uganda, North-West

Tanzania, North Kenya

Alcelaphus buselaphus cokei

Kenya and northern Tanzania

Alcelaphus buselaphus lichtensteini

Miombo woodlands of Tanzania

Measurements

head and body

200 (190—215) cm

height

130 (118—150) cm

tail

30 cm

weight

183 (175—218) kg males

167 (150—185) kg females

horns

50—70 cm

A. b. lelwel

head and body

195 (177—200) cm

height

107—120 cm (115 male ave.)
(112 female ave.)

tail

30 cm

weight

142 (129—171) kg males

126 (116—148) kg females

horns

45—59 cm

A. b. cokei

head and body

190 (160—203) cm

height

124 (119—136) cm

tail

46 (40—51) cm

weight

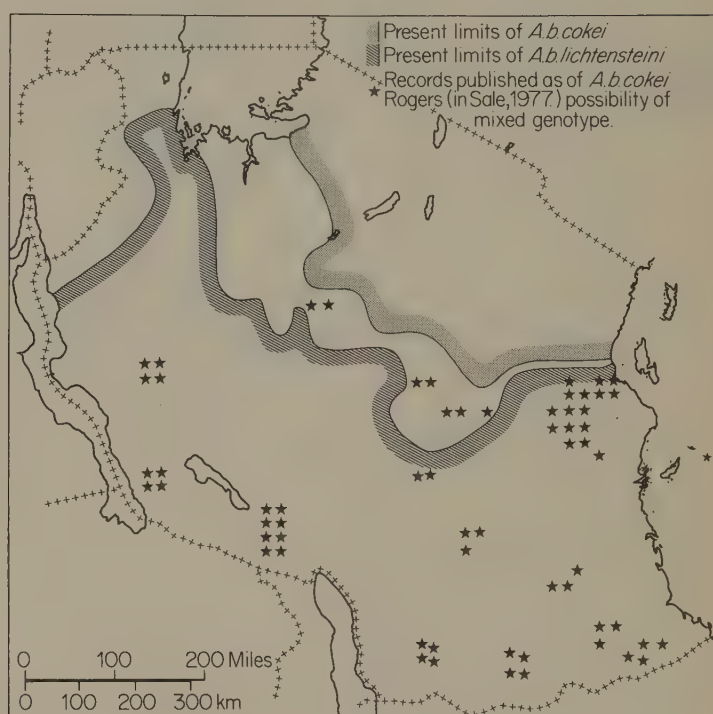
177 (157—204) kg males

165 (125—175) kg females

horns

45—62 cm

A. b. lichtensteini



*NOTE: Hybrids occur where the ranges of *A. b. lelwel* and *A. b. cokei* meet and mixed populations occur or formerly occurred in a belt between Mt Kenya and Lake Victoria. Types for *jacksoni*, *kongoni*, *nakurae*, *keniae* and *richtiei* came from this hybrid zone. They reflect various combinations of characters (mainly horn shape) of the two parental stocks.

Rodgers (in Sale, 1977) recorded pockets of *A. b. cokei* within the range of *A. b. lichtensteini* (see map above). No other observers of these populations have made this attribution but it is possible that the genotype of *A. b. cokei* is widespread in Tanzania populations of *A. b. lichtensteini*.



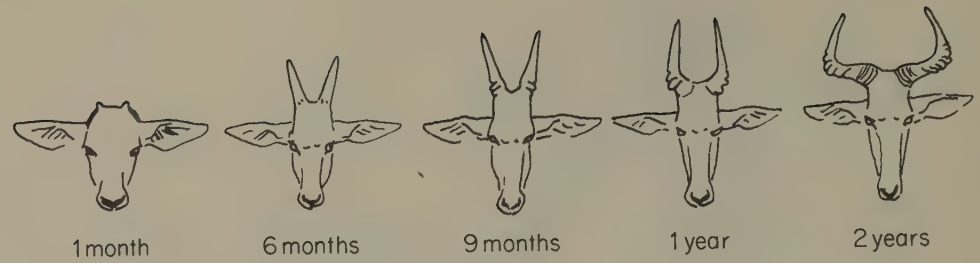


Hartebeest, Kongoni (*Alcelaphus buselaphus*)

The odd proportions of the hartebeest represent an interesting combination of adaptations. A grazer of coarse, long grasses it carries its compact, deep-chested trunk on legs which are slender and fairly long but are powered by massive shoulders and haunches.

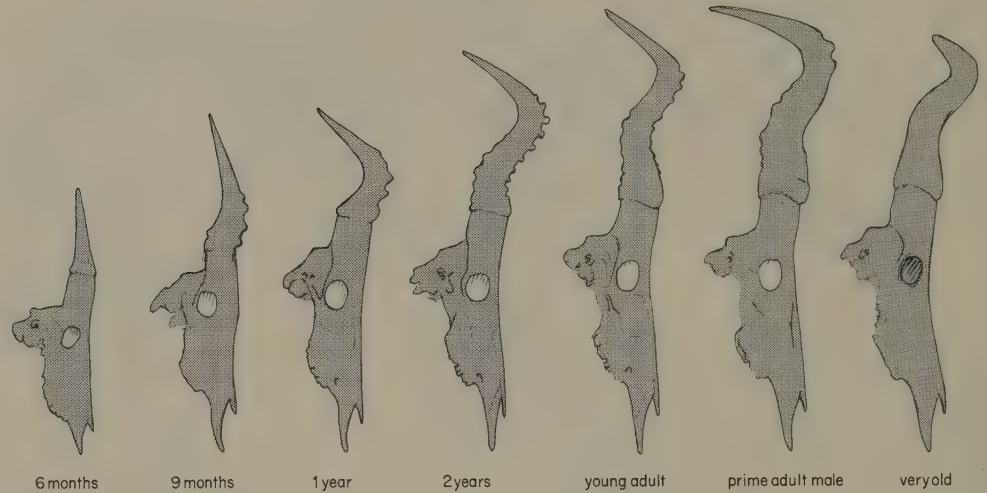
Highly conspicuous and generally sedentary in its habits, it offsets its vulnerability by being one of the fastest of antelopes. The peculiar elevation of the shoulder is caused by exceptional development of the thoracic vertebral spines. For a grazer, the neck is short in relation to its legs and is thick and powerful in males. The distance between shoulder and occiput has been effectively reduced (through compensatory elongation of the face, see p. 448) and the compactness of body and neck is a distinct advantage for both speedy galloping and fighting.

Above and opposite: *Alcelaphus buselaphus lichtensteini*.



Above: horn development in *Alcelaphus buselaphus cokei* (from Gosling, 1975).

Below: horn development in *Alcelaphus buselaphus lelwel* (aged by J. Bindernagel).

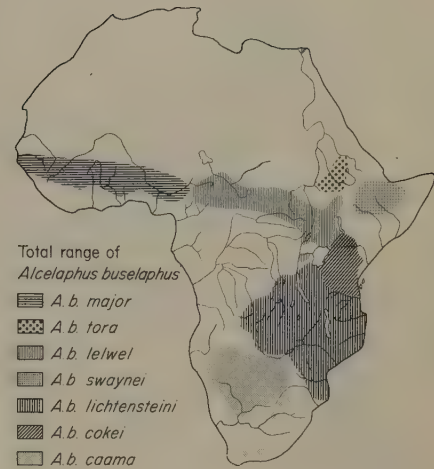
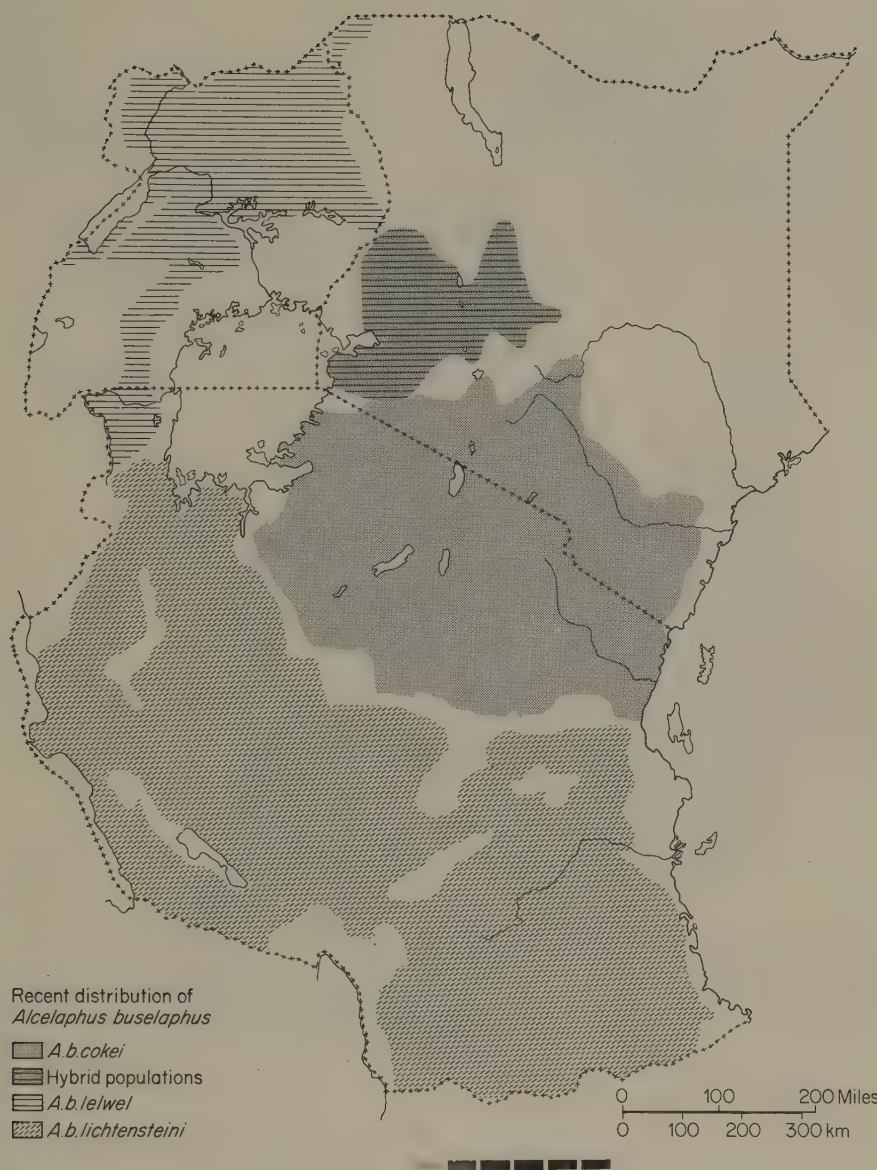


The horns differ considerably between races and there are differences in their style of fighting, but all hartebeest have heavy, hooked horns, the evolution of which has been discussed earlier (p. 440).

The hindquarters are very pale and the line of demarcation between haunches and the darker back coincides with the boundary of an animal's reach with its face glands. As self marking with secretion cannot reach the hindquarters without contortionist effort, these may have a less provocative (or at least a more neutral) connotation for other hartebeest. Since both sexes are horned from an early age, any device that reduces the chance of an attack by the aggressive males might be beneficial, as each territorial male represents a dangerous hazard that must be escaped or appeased.

Because the hammer-shaped head is so conspicuous, its carriage provides a good indication of the animal's intentions and it is no surprise to find small movements of the head and ears functioning as signals; (for example, a backward stretch of the rump is sometimes combined with a sharp retraction of the chin which produces a very characteristic and distinctive posture).

Conservative and sedentary habits have evidently inhibited gene flow, and some indication of this is the fact that a total of nearly fifty forms of *Alcelaphus* have been named. However, the eight species that were recognized by Sclater and Thomas (1894) do represent very distinct allopatric populations, each of which is adapted to local conditions and climate in a well-defined region or vegetation belt. In this work the eight populations



listed in the margin on this page have been classified as races of a single highly diversified species but at least one of these, *lichtensteini*, might justifiably be regarded as an incipient species.

In spite of being a prolific and, in some localities, a dominant species, the hartebeest has probably suffered the greatest contraction in range of all African ruminants: one major population is extinct and three others are drastically reduced. Because self-advertisement is an integral part of its social system and because it is so sedentary, the hartebeest is very easily hunted. Stanley-Price (1974) has shown that competition from cattle also has a direct effect on hartebeest numbers and has demonstrated very broad equivalence in their diets; so the expansion of cattle in Africa is almost certainly the primary cause of the species' decline. His study showed that



both these bulk-roughage grazers feed almost entirely on grass and are not very selective of either species or the component parts of grass in the dry season, and this tolerance of poor quality and difficult grazing at the worst time of the year has probably contributed to the dominance of hartebeest in the past. By acquiring a similar tolerance (with some help from man) cattle are favoured in the same habitats today.

Trials have shown that hartebeest select a higher proportion of grass leaves in the rains and sheaths are also selected at all times but particularly in defoliated swards. Selection is facilitated by the vertical movements and orientation of the hartebeest's head, for in very coarse clumps of grass stems and leaf can be rasped away by the teeth without cutting the toughest and more indigestible stems. Wilson (1966a) examined a large number of stomachs of Lichtenstein's hartebeest and found 95% grass but leaves or shoots were eaten off stumps or low shrubs of *Combretum* and other species.

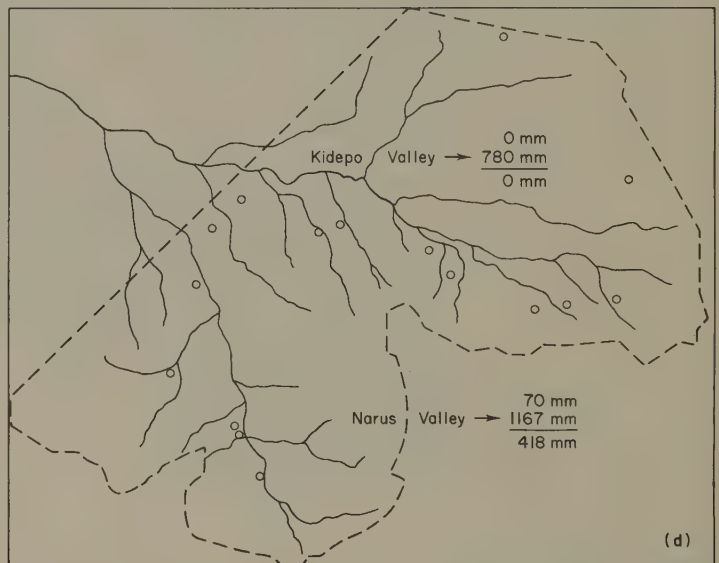
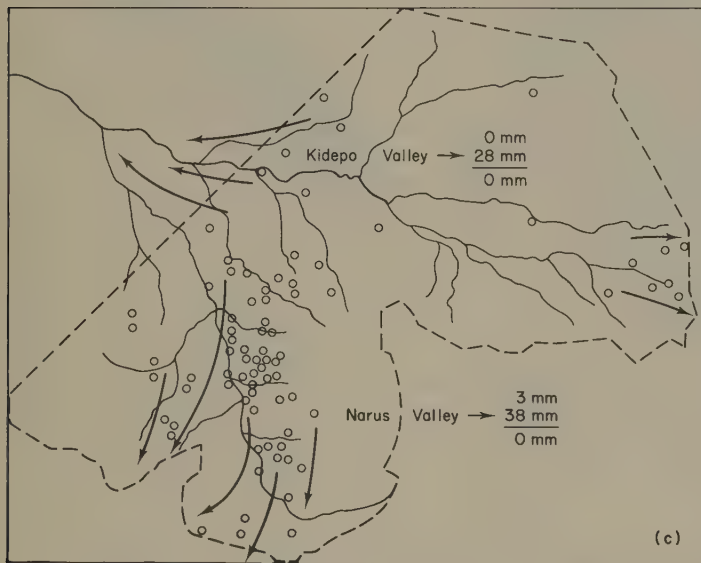
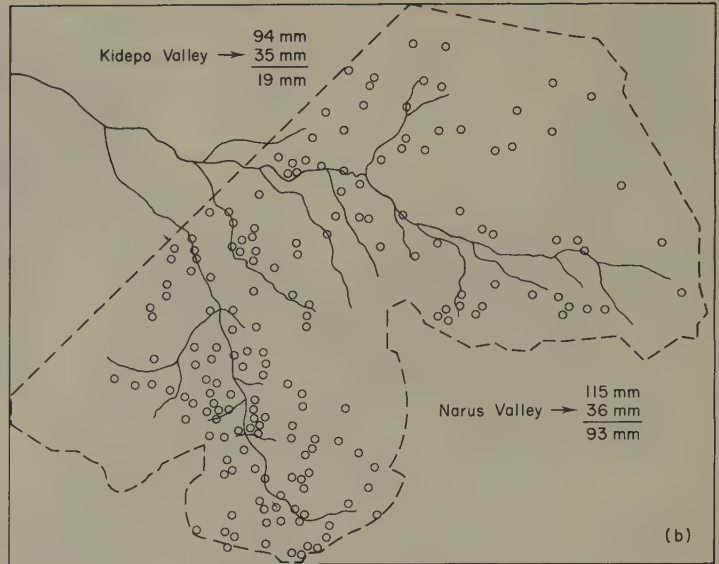


Lamprey (1963) recorded 3.75% of herbs and shrubs in the diet of *A. b. cokei*. Stewart and Stewart (1970) also noted very few greens or dicotyledons and there was a notable avoidance of *Cynodon* by hartebeest in their study.

Lamprey (1963b) characterized Coke's hartebeest as an "edge species"; Wilson (1966a) showed that Lichtenstein's hartebeest preferred ecotones and Gosling (1974a) identified the two most consistent features of hartebeest habitat as medium or long, coarse, grassland and an ecotone, usually between woods or scrub and open grassland.

I pointed out in Vol. I (pp. 32—33) that the miombo woodlands are laced by flat grassy cotton soil valleys or "mbugas" as well as lesser drainage lines and small glades. These open areas are in turn fringed by narrow strips of *Combretum* or *Acacia* savannas and hardpans (see pp. 35—36, Vol. I); these zones are the principal habitat of *A. b. lichtensteini* in Tanzania, while rather similar preferences are shown by *A. b. lelwel* in the *Isoberlinia* woodlands of the South Sudan and Uganda.

Alcelaphus buselaphus lichtensteini.



For a large grazer these are the least restrictive of the woodland communities; for the thin grasses of the well-drained woodlands dry out and are burnt off early in the dry season whilst the cotton soil mbugas are waterlogged for much of the wet season. The hartebeest are therefore to be found in these fringe communities most of the time but are able to move into the more extensive woodland and grassland areas at different periods of the year. The drainage lines are a source of fresh grazing and water for almost all the woodland ungulates at the end of the dry season, at which time *A. b. lichtensteini* often concentrate there together with zebras, waterbuck, gnu, sable or roan in parties of 20 or, in some localities (notably Ulanga), of up to 60 hartebeest together. In northern Uganda, much larger gatherings of *A. b. lelwel* gather in broad, well-watered valleys such as Narus in the Kidepo National Park.

The constraints of drought disappear with the arrival of the rains and the animals scatter widely (see b, p. 510), the females breaking up into small groups while most of the mature males become solitary and space themselves out in territories. As the rains and growth proceed there is a retreat from the longest grasses and most waterlogged soils up on to the better-drained slopes (see a, p. 510). It is here that edaphic conditions limit the growth of grass to a height that suits the hartebeest and it is these slopes that are in most permanent occupation (d, p. 510). During droughts or in areas where the hartebeest are strongly seasonal in their breeding, as in Kidepo, these factors may influence a population-dispersal pattern. For example, virtually all the females may move into thicker vegetation or to better watered pastures at the time they have their young, while attachment of the males to their territories may also be at a very low ebb four or five months after the rut. If this coincides with poor grazing and an absence of water, there may be a temporary but fairly general desertion of the slopes in favour of areas nearer water (c, p. 510). Because of the restricted extent of grassland patches within the miombo woodlands, *A. b. lichtensteini* tends to fragment into smaller social units than either *A. b. cokei* or *A. b. lelwel*. The waterlogged mbugas and hard-pan areas are completely deserted during the rains and there is a movement up into the top of the catena. Verheyen (1951) described a wholesale movement of herds up on to the Upemba Plateau at this time but in their Tanzanian habitat the relief is mostly on a small scale and movements are essentially short-range.

When the rains are over in May or June *A. b. lichtensteini* drift down to the low-lying areas again and the females are generally in small all-female groups when they have their young in July and August, but may gather in greater numbers as the available pastures shrink under the influence of fires, drought and grazing.

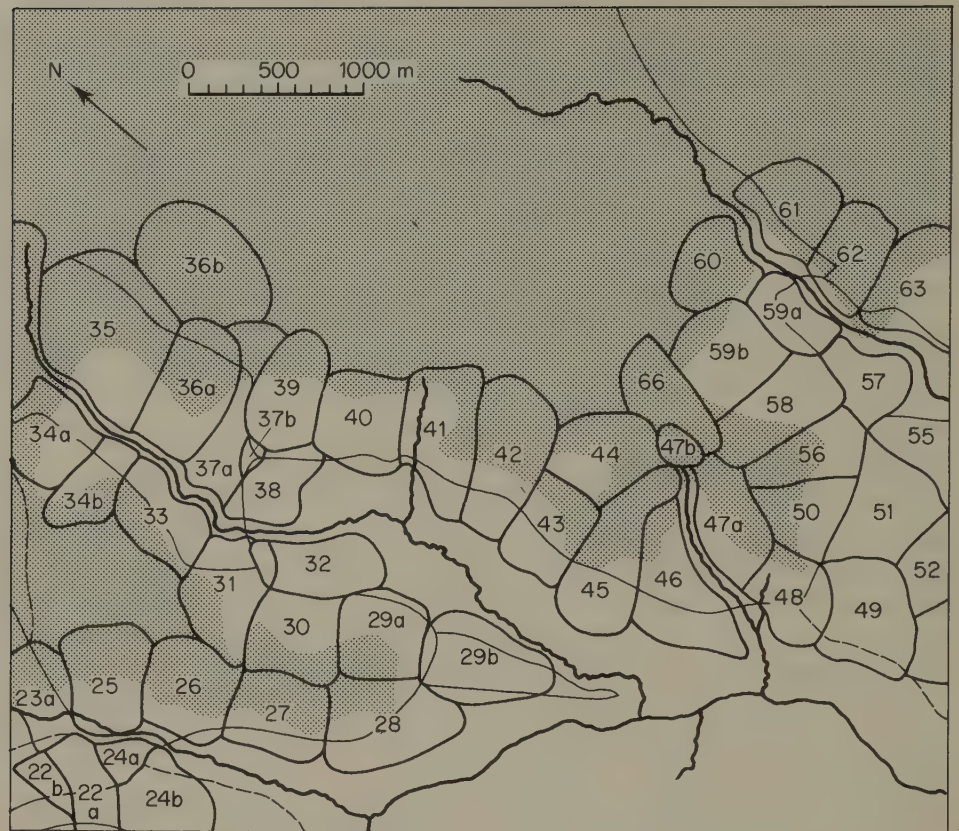
Hartebeest go to water regularly but in some circumstances territorial males appear to do without for quite long periods. In several localities hartebeest have been seen to drink in the early morning. Bindernagel (1968) followed a large gathering of *A. b. lelwel* which had been drinking at a river side at dawn. Made up of several groups, each consisting of five to twelve animals, this aggregation left the river soon after daybreak and moved off following the bottom of another valley. Between 2 and 5 km from the river, each herd or group split off and left the valley bottom to climb a slope to an area where the animals began to graze. Other observations suggest that this might be a regular pattern of activity during the dry season. Stanley-Price (1974) noted that the walk to water, which was often on alternate days for females and every three days for males, was at the expense of grazing time. *A. b. lichtensteini* usually rest under shade during hot weather and may lie down in small groups. Dowsett (1966b) also found evidence of them lying down during the night.

In the Nairobi Park, *A. b. cokei* have three feeding periods, which are spaced at nearly equal intervals throughout the 24 hours, but higher midday temperatures do reduce the amount of time spent grazing during the heat of the day.

While females are free to seek the best grazing in their home range, the activities of territorial males are much more circumscribed by their territory.

Opposite page: hartebeest (*Alcelaphus buselaphus*) distributions in the Kidepo and Narus Valleys of North Uganda. Rainfall for the month shown for each valley (with previous and subsequent months also indicated) (data from I. Ross). a. Preferred hartebeest habitats (based on cluster analysis and probably indicative of male territories). The number of months in which hartebeest were recorded is indicated (out of 23). Note preference for lower slopes of valleys. b. May 1968. Wide dispersal during month of peak territorial activity and mating. Grass and soil conditions normally optimal for the species during May. c. October 1968. General drift towards moister valleys, scrubs or woodlands. Minimal territorial activity and most females heavily pregnant. d. January 1969. Scattered animals (principally males back on their territories). Birth season; females mostly in neighbouring areas. (Note: in some years many births in Narus Valley woodlands.)

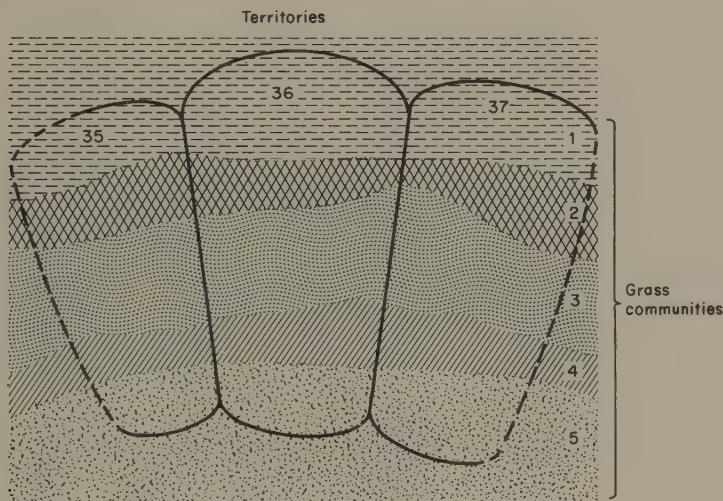
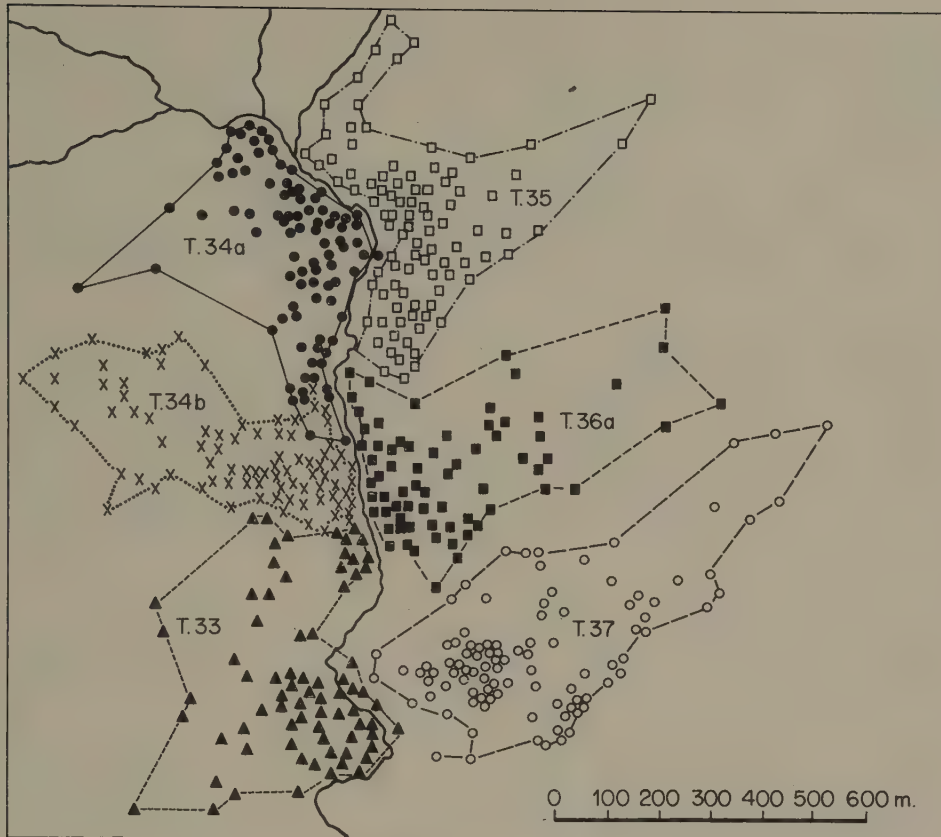
Territories strung along sides of valleys in Nairobi National Park during 1967. Stipple indicates plateau areas with homogeneous well-bushes vegetation. Irregular lines trace stream beds. Thin lines show Park tracks (from Gosling, 1975).



Gosling (1976) showed that an increase in the number of males could be correlated with a reduction in the size of territories, while the quality of the range and the severity of seasonal changes have a direct influence on the distances animals move and the area of home ranges. While conditions are at their best in the well-grassed, well-watered Nairobi National Park the females of *A. b. cokei* have ranges of about 5 sq. km, an area that may include 20 to 30 male territories, the mean size of which has been estimated at 0.31 sq. km (Gosling, 1974a, b). Gosling found that the males' territories vary considerably not only in size but also in the amount of time they are occupied; furthermore, the most highly favoured ones tend to be held by the fittest males while the most peripheral ones are held by older, weaker males which are unable to regain the territories they held in their prime.

Territories are often strung out side by side along the slopes of valleys, each one embracing a variety of catenary zones in which the grass species, its height and the length of its growing season differ according to drainage and other edaphic conditions. The most open areas and shortest grass are on the ridges, rises or plateaux, where the territorial male tends to station himself. In Tanzania, I have often noted single males of *A. b. lichtensteini* standing on open, elevated areas along ridges in the miombo, but this is seasonal. Millais in 1895 noted ground scrapes and the attachment such males had for their stamping grounds.

Spacing depends on the density of the hartebeest population and on the habitat. Gosling was able to show that ecotone territories in the Nairobi



Above: daily point observations of six individually recognizable territorial males (Gosling, 1975).

Left: Territory orientation in relation to grass communities (after Gosling, 1974a).

Park, which are often only 200–800 m apart, are almost permanently occupied, whereas males are in possession only half the time in their less favourably placed territories and he classified the different types into pivotal, axial and peripheral territories. In the Nairobi Park the male's attachment to his territory is likely to be reinforced by a year-long water supply in the nearby dams and may be linked with very extended breeding in *A. b. cokei*. In this area there is a mating peak in June but there is a certain amount of sexual activity throughout the year. In contrast, *A. b. lelwel* in Uganda

has a short and well-defined mating season from late April to June and the males appear to be less tied to their territories, particularly during periods of drought, when they may follow the heavily pregnant females in a general drift down to moister valleys or to concentrate around springs and water-holes.

Gosling (1974a, b) frequently saw the mating activity of Coke's hartebeest interrupted by intruding males and he thought that high densities probably disrupted courtship and reduced the chances of successful copulation.

There are very few births of *A. b. cokei* in September and October, which betrays that mating is at a minimum during the driest months of the year, January and February, when the population is also most concentrated. How this might relate to the adults' condition at conception and to the long-term survival of calves remains to be demonstrated. It is known that hartebeest have been extremely numerous in several parts of Africa in the past and Stanley-Price (1974) recorded as many as 17.8 per sq. km. Much remains to be learnt about territorialism as a spacing mechanism at very high densities.

Adult females do not form permanent associations with other adults but they are occasionally accompanied by up to four generations of their young (Gosling, 1974a, b). Female offspring can remain attached to their mothers up to the time they have calves of their own or up to the age of three. Male calves may remain with their mothers from the age of ten months to three years, by which time they have adult-sized horns (Gosling, 1974a, b). Testes and epididymis sections suggest that they can be sexually mature at twelve months (Bindernagel, 1968), so the prolonged bond is unusual and interesting, for these young males have not been recorded as attempting to mate in spite of their physiological capacity to do so.

Their presence in female groups is an intense provocation to territorial *A. b. lelwel* males during the rutting seasons and I have frequently seen them at this time so preoccupied with the pursuit of both eighteen- and six-months-old males that both females and young were driven out of the territory. The male usually tries to skirt the females to reach the young, which tend to shelter behind their protective and defensive mothers but the male occasionally goes for the female as well.

Females are not entirely submissive in these circumstances and I once saw three mothers effectively distract a persistently aggressive male, one engaging him in a horn clash every time he went for her young, while the mothers of the other two victims alternatively prodded his flanks and feinted before he could follow up his attack. The apparently concerted nature of the three mothers' defence was probably due to the male's having pursued all their young in quick succession and the co-operation may have been coincidental. Females also protect their young from other females, threaten them and very occasionally fight one another. In Zambia, Dowsett (1966b) recorded fierce fighting and expulsion of young males by dominant bulls during the rutting period of *A. b. lichtensteini* (mid October to early January) and he saw aggressive incidents, including sparring, charging and chasing between females. (He also saw one female trying to mount another.) Backhaus (1959) suggested that such incidents are evidence of a female hierarchy and Gosling (personal communication) thought that females have



dominance relationships and that our understanding of the animals' social organization will require a closer definition of the nature of inter-female relationships. In a generally aggressive society it is clear that all classes of animals need horns.

Outside the rut territorial males of *A. b. lelwel* are less aggressive towards the young. In the less strictly seasonal *A. b. cokei* the relationship has been described by Gosling (1974a). "Up to ten months of age there were no stereotyped interactions between male offspring and territorial males. After this age, when the first curve of the horns appeared, the behaviour of young males underwent a striking change. This change did not occur in females. When territorial males approached male offspring assumed the Head-in posture and emitted juvenile 'quack' vocalizations." Gosling goes on to remark that this behaviour may inhibit male aggression and, with the prolongation of the mother-male offspring bond, serves to gain access to the best pastures for a longer period. There is evidence that young males that have just been expelled from the herd are most vulnerable to predators, resulting in an adult sex ratio of about three females to two males. So the risk of predation might make a prolonged adolescence advantageous. Every time the mother has another calf the young male is prevented from approaching closely and other females in a group will often chase off young males

Alcelaphus buselaphus lelwel.

that come near them. Where there has been a seasonal peak of births, those expelled represent an entire age class and they tend to gravitate towards one another and form bachelor parties. Age-classes are not conspicuous in the non-seasonal Coke's hartebeest and bachelors are of mixed ages. Gosling recorded that bachelors as a whole ranged over 6.7 to 10.3 sq. km in the Nairobi National Park and he suggested that they might be forced to range more widely because of exclusion from the best pastures by territorials.

The bachelor herds are loose and open aggregations numbering up to 100 animals. There is a great deal of interaction amongst individuals; they rub faces on the ground and on vegetation as well as on their own and one another's bodies, they touch heads, wrestle with their horns and often finish with clashes in which the contestants drop to their knees and, tucking their long faces into their chests, hammer their horns together. Gosling (1974) was able to recognize many individuals and, by watching the outcome of numerous encounters, demonstrated a linear hierarchy in which no reversals of dominance were recorded. Before the animals reached their full size dominance was directly related to size. After the age of three, individual males achieved progressively higher status until they started to isolate themselves or completely left the vicinity of male groups and moved about on their own. Sometimes they remained in one place for a day or two (often in scrub) but then moved on.

This behaviour is a prelude to the occupation of a territory and Gosling (1974a) has remarked that an important function for the hierarchical and gregarious phase may be to establish a position of dominance over all potential competitors. He saw the change from non-territorial to territorial existence as a continuum. For example, the territorial male may in some circumstances join groups of bachelors where he immediately assumes the top position in the hierarchy, a status that is visibly demonstrated when he stands on the top of a territory with the others clustered below.

Once the males in Gosling's study area had established territories, he found that they remained loyal to the area of their first tenure. However, both drought and waterlogging force bulls to leave their territories for variable periods of time and on their return they frequently find an usurper, whereupon there is ritualized display and very often a fight which is decisive, leaving one or the other animal in undisputed possession. These tend to be serious fights and they are sometimes attended by severe injuries or even the death of one contestant. The vicissitudes of seasons and the decline in physical condition of territorial bulls combine to ensure that there is small chance of a long tenure. Gosling calculated that 44% of territorial occupations recorded in the Nairobi Park lasted less than three months. Over the three years of his study only two males were found to have retained their territories continuously.

Where there is a distinct rutting season, as in Uganda, the majority of territories are held for an even shorter period and the seasons' constraints are obvious. The dense concentrations of *A. b. lelwel* around water during the drought break up as soon as the first rains appear and flushes of green growth allow animals to scatter over the widest possible area and offer most adult males the opportunity to claim a territory. The dense grass growth of the later rains and the waterlogging of the ground drive the animals out

of the valley bottoms and lead to scattered concentrations on higher ground (see map). In the intervening period all adult females are inseminated. Oestrus and conception may be influenced by hormonal changes deriving from a green grass diet but it is also likely that spatial emancipation is a factor in the successful operation of the male territorial system. The brief period of ideal and widespread feeding conditions may therefore answer different needs in the two sexes and it may be the combination of the two that defines the breeding season so clearly in Uganda.



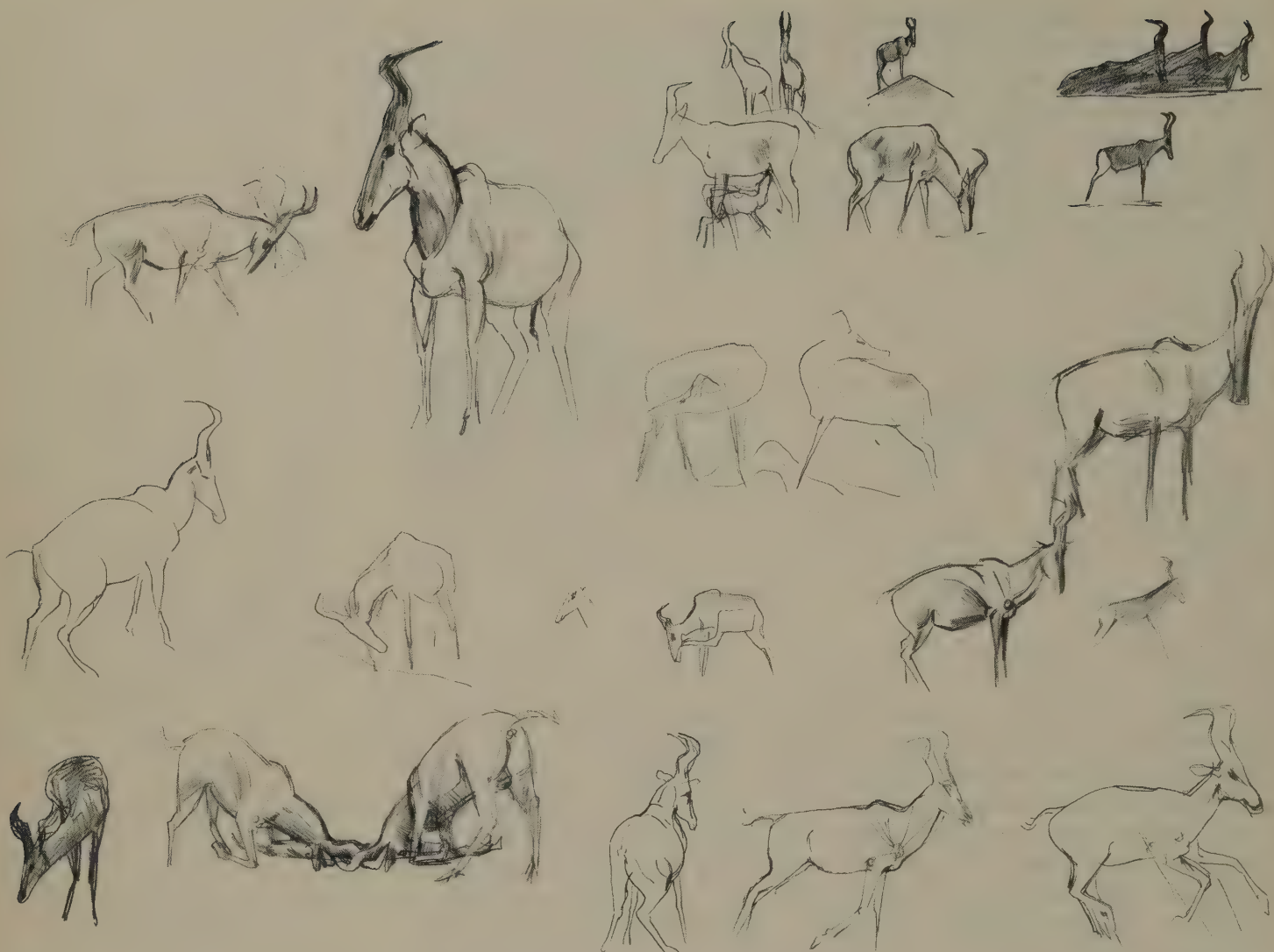
Female and male
Alcelaphus baselaphus lelwel.

The intensity of territorial behaviour is very variable but males are generally at their most intolerant during the height of the rut.

Vision is a dominant sense and it is clearly the sight of other males that precipitates action but the degree of intolerance and the distance over which the territorial will react seem to be influenced not only by the timing of a local breeding pattern but also by the density of the population and by the posture and actions of neighbours.

The very widely spaced out males of *A. b. lichtensteini* are exceptionally vigilant and make a loud snort or stamp the foreleg if disturbed. This behaviour alerts any females and young that may be nearby and may also serve to provoke a reaction in a potential intruder. Once an animal takes to flight others follow behind, generally strung out in a line but males often veer off and run in a wide circle, probably out of reluctance to invade another territory or to leave their own.

Gosling (1974a) pointed out that the behaviour of an intruder, its proximity and the territory holders' activity immediately before the intruder's arrival all influence the residents' reaction. Climatic effects are predictable in that the hotter the weather the less frequent the responses. When the Nairobi Park population was over 17 per sq. km Stanley-Price (1974) remarked that the males were extremely aggressive within their tightly packed territories, but I have seen widely-spaced territorials of *A. b. lelwel* that were equally aggressive during the rut, galloping at intruders from a distance of about half a kilometre and fights were frequently precipitated at this time by the passage of a vehicle, presumably frightening one animal into another's territory. On the other hand, I noticed that interactions appeared to be at a lower intensity outside the mating season.



Alcelaphus buselaphus leleu.

A territorial male entering a boundary area very often attracts the attention of his neighbour, which then approaches and halts some metres away; a ritualized ceremony follows that has much in common with those of gazelles and neotragines. One or both animals may paw at the ground which has already been scraped bare, or if there is a convenient termitary they may sniff and rub their faces or horns on the mound, the earthen surfaces of which are worn down by repeated grating. Scraping with the hooves is usually followed by a spasm of face rubbing on bended knees and then a hasty return to a quadrupedal stance. Self-anointment (see p. 450) is very common. The animal flings its face vigorously against the flanks or shoulder (I have noticed here a tendency for what appears to be the senior animal to rub its back, whereas less confident animals often anoint their lower flanks or scratch their bowed head with the hindlegs, but this might have been coincidental). At this stage one of the animals often defaecates on a long-established pile of dung and after more sniffing and self-anointing,

rubbing and pawing, the other bull defaecates and the two are often sufficiently close to sniff one another's faces, nibble and rub one another on the neck, after which they might touch horns or even spar briefly, but more usually they turn away and drift apart. As with other antelope species, dung piles are made both within the territory and along the peripheries, but Gosling noted that there are fewer within the territorial area than in the boundary zone. Since dung piles are only scraped when on the boundary, this behaviour must be linked with their use by both territorials, as each superimposes his scent upon that of the other. (Urination has not been ritualized in this species.) After chasing off an intruder, a male will often return to his territory with a bouncy galloping gait and then ostentatiously deposit dung on one of his piles. (This gait is adopted when animals are excited or disturbed and is often seen after rain.) However, dung cannot be produced repeatedly and voluntarily so the territory holder commonly returns and taking up a position close to one of the landmarks of his ground, (dung pile, scrape or territory) arches his back down and stretches the hindlegs in what looks like a token defaecation. The hindlegs can either be flexed back in a relatively brief action or alternatively the animal remains in a static posture with his legs placed unnaturally far back. While this gesture may be a symbolic defaecation, I have also seen it in an indistinguishable form in females and calves as well as bulls, and it should be remembered that hindquarters are the principal focus of interest in the social encounters of most mammals. As I remarked earlier, the hartebeest's rump is devoid of its own facial secretions. On the other hand, a female's rump is sometimes rubbed by the face of a courting male. The rump-stretch



Alcelaphus buselaphus lelwel, rump stretching.

certainly seems to act as an attractive stimulus to other hartebeest. Males assume this position in the midst of courtship (often just before mounting) and, after watching repeated copulations between one pair of hartebeest, Backhaus (1959) recorded the female flexing her hindlegs while standing close to her consort. Because there are several contexts for the backleg stretch and several possible origins can be suggested, the gesture might be dismissed as incidental. However, it is peculiarly prominent in the behaviour of alcelaphines and I believe that this gesture combines with the pale rump colouring to offer a generalized attractive signal to other hartebeest.

I have, for instance, seen adult male *A. b. lelwel* change their aggressive demeanour to a neutral approach when a calf stretched back its legs and pulled its chin in. Many hierarchical societies employ appeasing behaviour but the aggression associated with male territorial behaviour also has the potentially counterproductive effect of frightening off the females. This can happen directly if the female, which is horned and not very obviously differentiated from a male is pursued, or indirectly if she follows her persecuted young. Since it is in the interest of the species to avoid this, the females and young ought to be capable of disarming or at least modifying the aggression of a territorial male through their own behaviour. Likewise, the males need to be, if not positively attractive, at least not totally alarming.

The light colouring of the rump is a natural focus of attention and distracts from the potentially provocative horns to the opposite pole of the body. If the head is lowered and the rump presented, the light area and switching tail are the most prominent features of the animal, but if the hindlegs are stretched back the light falls more directly on to these pale surfaces and increases the conspicuousness of the hindquarters. Since the posture contrasts with the normal, this alone is likely to attract attention, and a bull standing with erect head and stretched rump is displaying both aggressive and attractive signals.

It is perhaps the fact that both females and rival males are his potential public that influences the apparent duality of this male alcelaphine posture.

Any single female together with her young will form loose associations with other females. In the Nairobi Park where females range over about 20—30 male territories good grazing in a well-favoured territory may induce females to remain in one locality, but the males' herding also influences their movements and the females very often deliberately approach a territorial male, which suggests that his self-advertisement is actually attractive. It is possible that a direct approach and close association with a territorial male avoids the harassment of being threatened and herded.

Territorial males sniff at the genitalia of visiting females but do not (or are unable to) make a *flehmen* lip-curl. If signs of oestrus are identified, the male shows intense interest, following or circling the female persistently with ears strongly depressed. Attempts at escape are confronted with threats from tossing horns and blocking the way by the male. When the courtship is more ritualized, the male simply stands in lateral presentation in front of the female before resuming the inspection of her genitalia which is eventually permitted by the female. Gosling (personal communication) has noted that the lateral presentation assumes explicitly aggressive connotations when the male tosses his horns and tilts them at the female and, in such cases, he never saw a successful mating. Once the female is immobile the male can mount and, although the copulation is very brief, it may be repeated many times. Courtship is immediately interrupted if another male approaches, and Gosling recorded that intruders were always chased and proved subdominant. Although such interferences sometimes result in females leaving the territory the male usually finds the oestrous female again and mating behaviour continues.

Gestation is about nine months and the calves are often born during

the worst time of the year. The mother usually seeks to have her offspring in long grass or near thickets but this is not always possible.

Both Mitchell (1965a) and Ansell (1971) have described newborn calves of *A. b. lichtensteini* lying up in small clumps of grass or beside leafless bushes in burnt or open country. The latter author witnessed a leopard carry off a calf and in an apt illustration of the newborns' vulnerability he described being approached quite fearlessly by a bleating calf with a still wet umbilical cord. Verheyen (1951) described such a calf following his lorry, whereupon the mother made repeated approaches and swung into lateral presentation and jumped lightly up and down in the manner of a goat. The calf was finally diverted by the mother interposing herself between it and the moving vehicle. The lateral display and jumping movements reported in this incident indicate something of the predominance that visual communication has acquired in the life of the hartebeest. In Aswa Lolim, almost every female *A. b. lelwel* is likely to calve once a year, and Bindernagel (1968) counting about a month after the end of the calving season found that about 21% of the total population were calves. As the total number of adult females is probably little short of 40%, a high proportion of newly born calves are probably lost to the hyaenas that are numerous in this open plains habitat. Bindernagel found little change in the ratio of young surviving to the end of the year and the calves did not seem to be more vulnerable than adults once they had emerged from their lying-out period. Gosling (1974) estimated that 70% of *A. b. cokei* survive their first year in the Nairobi Park. In this Park McLaughlin (1970) reckoned 9% of the annual calf crop is taken by cheetahs. The difference between the two areas may lie in the presence of thick vegetation in which the Nairobi females can give birth and hide their young and the near extermination of hyaenas in that area.

In the Kafue Park, Dowsett recorded 70% of all Lichtenstein's hartebeest kills as being the work of lions, the victims being mostly calves and yearlings and with a heavy preponderance of males at all times except for the calving season, when nearly four times as many females were killed as males.

Calves seek the company of other young and it is not uncommon to see more calves than females in nursery groups. This habit has often given rise to reports of twins or triplets. The tendency to attach themselves to other antelopes occasionally causes the young to run with other species such as impala or kob. They are weaned by the age of four months. Adult horn size is reached in two years and maximum weight in about four years but the age of maturity appears to vary. Bindernagel found that *A. b. lelwel* produced their first calves at the age of two years and testes sections showed that males were sexually mature by the time they were one year old. In contrast, Stanley-Price (1974) reckoned that most of the Nairobi population of *A. b. cokei* did not breed until their fourth year and he correlated the relatively slow rate of growth and late maturity with the poor-quality diet available at the time of his study.

Juveniles are more vocal than adults and make quacking distress calls that are commonly uttered when the calf is pursued or threatened. This call is closely associated with the appeasing behaviour of an inferior animal and is occasionally heard in similar contexts in adults. Gosling has described mothers making a quavering bleat when searching for a calf and he heard

a peculiar coughing call when a herd was on the run. A loud snort made by any class alerts all animals within hearing and is usually uttered by an alert standing animal at any disturbance or predator.

When the young males are finally forced to abandon the company of their mothers, they are not only frequently damaged by their persecutors, the territorial males, but are denied access to much of the best grazing, and Gosling, Stanley-Price, Bindernagel and Dowsett have published evidence for measurable drops in the numbers of male yearlings, usually caused by their increased vulnerability to large carnivores. In the Nairobi Park, Gosling was able to show that transitional periods between one social state and another rendered males peculiarly vulnerable to lions and cheetahs. Both young males and very old territorial expellees tended to find refuge in overgrown areas, where presumably they escaped the attention of rivals, only to fall to predators in unfamiliar terrain where the value of their acute eyesight and speed are diminished.

Adult hartebeest are killed by lions, hyaenas, leopards and wild dogs, while cheetahs take immature animals and jackals sometimes kill small calves. Newly born calves crouch in response to danger. Gosling found old males particularly vulnerable to lions but the hartebeest occasionally fight back and a leopard has been recorded dying of its wounds near the hartebeest it had killed. Lions are often watched very closely but without flight, even after they have made a charge (Schaller, 1972b). I have followed the blood trail of a hartebeest being run down by wild dogs which ran downhill over about 2 km of rough and stony ground, which suggests a remarkable stamina.

The hartebeest suffers from a wide variety of parasites (see appendix), including the larvae of a fly which lives in the nasal septa and in the hollow cavities of the horn pedicel.

The last 15 years have seen two major population crashes of *A. b. cokei* in Kenya and northern Tanzania, one during the drought of 1961 and the other in 1973. In the latter drought dam water was available to some of the animals in the national parks but, nonetheless, they died of starvation as did the cattle. Previous to the 1961 drought the Nairobi Park had been heavily grazed by domestic stock and gnu, which maintained short grass conditions over large areas. The drought dropped both gnu and hartebeest to a population of about 700 animals, but the relief of grazing pressure encouraged a rank grass growth and this development was decidedly detrimental to the gnu and their numbers continued to drop still further in the following years. The hartebeest, instead, increased enormously and with the removal of sheep and goats from the park in 1967 the hartebeest became the dominant herbivore, achieving a population of 2,100 in 1972 before its crash to an all-time low in 1974.

The hartebeest's elaborate social life and direct competition with cattle makes it an unlikely candidate for systematic domestication. The ancient Egyptians are said to have domesticated them and there are bas-relief representations of captives, but the practice seems not to have been particularly successful. The animal is rare in zoos, partly because breeding is difficult, and partly because the animals are dangerous to one another and to keepers when in confinement.

A. b. lichtensteini is in retreat wherever settlement has been able to move

into the miombo woodlands, particularly since the first choice of land for cultivation is their own favourite zone of the fertile lower slopes. However, the animals' outstanding alertness, their occupation of the tse-tse fly's primary habitat and their wide scatter through difficult hunting country gives them some protection from conventional shooting.

In spite of the hartebeest representing one of the most recent and the most highly evolved of ungulates and in spite of its ability to reach high densities, it is likely that its range will continue to contract and that an overall depletion of numbers will continue. This expectation is borne out by widespread observations of the species' decline wherever there is intensive cattle keeping. The possibility of their co-existence on large scale ranches should be investigated before it is too late, as it is widely acknowledged that hartebeest meat has excellent flavour and the animal is in any case one of the most interesting and successful members of the indigenous African fauna.





**Gnu,
Wildebeest
(*Connochaetes
taurinus*)**

**Family
Order
Local names**

Nyumbu (Kiswahili), Ingumbu (Luhya),
Inyimba (Ishinyiha), Mbushi (Kisukuma),
Mbusi (Kinyaturu), Nchovu (Kizigua),
Isamaga (Jita), Oinkat (Masai), Ingat
(Samburu), Ngatata (Kikuyu, Kikamba),
Riwo, Korokit (Lwo).

Bovidae
Artiodactyla

**Measurements
head and body**

194—209 cm

height

128—140 cm

tail

45—56 cm

weight

200 (150—270) kg males

160 (118—208) kg females

(averages vary regionally)

horns

40—73 cm

Gnu, Wildebeest (*Connochaetes taurinus*)

Races

Connochaetes taurinus albo-jubatus

South Kenya and North
Tanzania

Connochaetes taurinus johnstoni

Southern Tanzania

The true affinities of the gnu are so effectively disguised by its dumpy proportions, beard and mane that at least one naturalist has been persuaded that it has a bovine relationship. I have discussed earlier the animal's peculiar colouring and proportions in the context of its alcelaphine relations (p. 448) and illustrated the wide muscular mouth with its small gape and square lips.

This shape of mouth is one of the more obvious symptoms of an important limitation—dependence on short grass. At times a gnu may be forced to strip leaves from tall stems but this is only a forced and temporary expedient to see the animal through a bad time of the year. Persistent rank growth induced by prolonged rains is useless to the gnu and this is a major factor explaining the absence of gnu from many areas of equatorial Africa, including Uganda. On the other hand, the gnu is dependent on moist grass or, failing that, a reliable water supply and it is this limitation that has contributed to the species' absence from the driest areas of Kenya.

The gnu is widely distributed in various open bushlands and grasslands of the southern savannas but is totally absent from the northern savanna region. Because the animal needs habitats that are neither too dry nor too wet, it is possible that its invasion of suitable areas of the northern savannas has been inhibited by the narrowness of such belts today, by their climatic instability and also by broad barriers of forest or long grass. It would be interesting to know if the gnu ranged further north before the Sahara reached its present extent. A gnu-like animal appears on a carved slate of about 3,000 B.C. from Hierakonopolis (Petrie, 1953), which suggests that the animal might have been familiar to the ancient Egyptians but it tells us nothing about past distributions.

With the animal absent from such wide areas of Africa it is surprising to find it inhabiting rather varied habitats in south-eastern Africa. For example it lives in overgrazed areas within relatively dense bush, in open *Brachystegia* and *Combretum* woodlands on flood plains and on more elevated grassy plateaux. Common to all these areas, however, is access to water and a short herb layer. Pruning by herbivores and fire maintain grass at short heights, while shade, rainfall, the water table and local edaphic conditions may all inhibit growth or produce a variety of different types of lawn, any of which may suit the gnu. There is no gnu habitat, however, in which one or more of these factors is not a major influence on the range even if these habitats will only support small resident populations. Bell (1971) has discussed the gnu's place in the Serengeti ecosystem and suggested that it is limited as much by a reduction of the range's carrying



Total range of
Connochaetes taurinus



capacity during the height of the rains as by a shortage of food in the dry season. In support of this he points to the fact that the herds of migratory gnu share their dry season range with the already large population of resident gnu in the western corridor or Kirawira area (near lake). Duncan (1974) assessed that 95% of the standing short and medium length pasture was removed after two dry months of non-growth and that 50% of the long grass was stripped of its leaf, confirming that this western area of the Serengeti Park may have a higher carrying capacity for gnu in the dry season than it has in the wet. Bell has remarked on the freak of geology and climate that has juxtaposed this area with the vast plains that burst with short grasses and herbs for the period of the rains only to become waterless and empty with the arrival of the dry season. Gnu, of all the larger ungulates, are best able to use this relatively short-lived resource not

only because they are adapted to the vegetation but surrounding habitats are rich enough to support the gnu during the dry season while the animals have a sufficiently plastic social system to congregate in vast and dense numbers and to make the necessary migration.

Small groups of gnu make short-range movements in a similar fashion to topi and hartebeest, taking advantage of local variations in topography to exploit the best grass available in any season. The Serengeti migration is a similar movement by many more animals on a huge scale. Many hundreds of thousands of gnu desert the open plains when the grass stops growing and move towards Lake Victoria, often moving in thick clouds of dust, for which their flapped, hair-lined nostrils are well adapted. By the time the dry season is over, the gnu have usually grazed their range nearly bare and they embark on their return journey to the plains in pouring rain. These facts convey little idea of the impact of these mass movements on the area. The vegetation along their route is trampled and eaten flat. So relentless is their advance that they swim rivers and Lake Lagaja in solid masses, crushing and drowning one another and leaving an aftermath of dead and maimed animals and lost calves that feed carnivores and vultures for weeks. These dependents and swarms of black flies accompany the herds. Indeed, as the dominant large animal the gnu are a major influence on the lives of most of the lesser fauna, either as competitors monopolizing the major vegetational resources, as a source of food themselves or as a physical force assailing the habitat. A vivid record of this unique cycle is Alan Root's film, *The Year of the Wildebeest*. The Serengeti migration has an established and seasonal pattern in which tradition evidently plays its part. Herds set off towards distant thunder clouds, apparently reacting to the sight or sound and perhaps also to the smell of rain, but in western Masailand they were seen not to attempt a trek towards rain falling on the inaccessible Siria escarpment. Talbot and Talbot (1963b) suggested that this might be due to previous failures by older animals which inhibited a response towards the sight of nearby rain. Nonetheless, Talbot twice saw herds of 3,000 gnu set off towards rain clouds they could not reach, thereby giving themselves fruitless walks of about 200 km.

Watson (1969) has stressed that for most of the year there is a minimum of social organization in the migratory herds and that the low level of social organization is related to the large numbers. However, Estes (1969) studying a relatively stable population in the Ngorongoro crater found a typically alcelaphine territorial system.

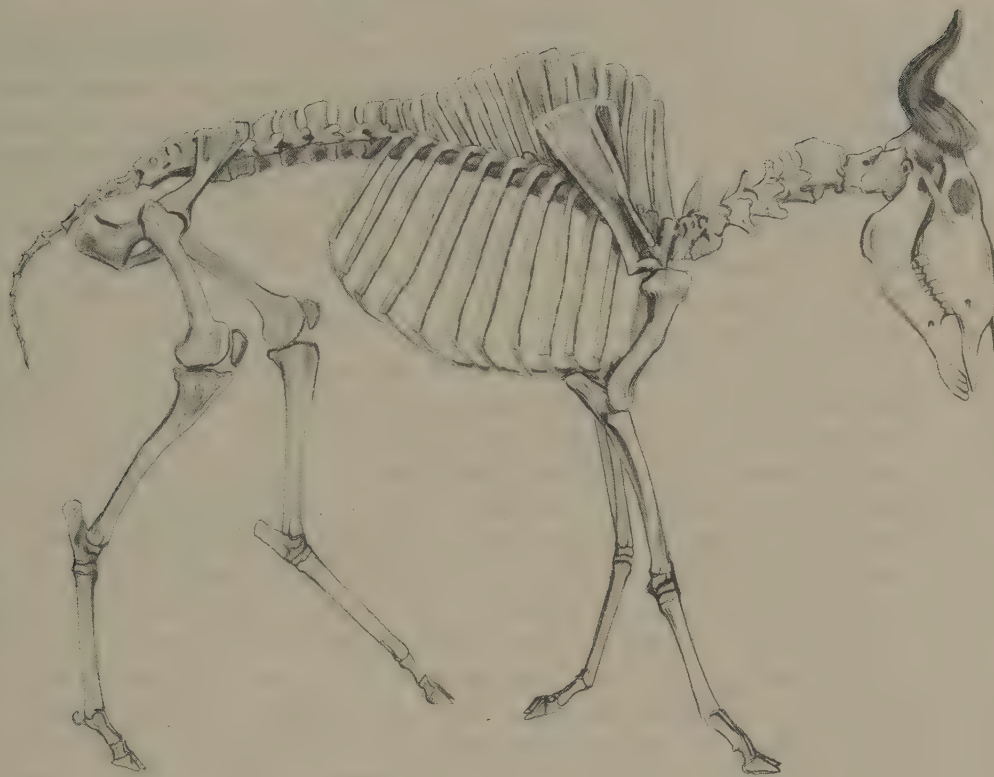
The females follow the grazing freely, while the territorial males, which form less than half the total male population, remain spaced out all over the crater in more or less permanent territories. Bachelor herds circulate along the peripheries of the territories or move with large aggregations of females, where they are less easily harassed by the territorial males. Males in the migratory Serengeti population are swept along by the movements of the mass but the May migration coincides with the rut and the bulls continuously try to detain and herd females in temporary territories and succeed in doing so as soon as there is any checking of movement.

Estes found that even temporary territories were related to a fixed piece of ground and the holders displayed rituals and demonstrative marking. A



tree or a termillary forms a favourite focus for a gnu's territory and migrating bulls often stand beneath an acacia or on a mound or display herding behaviour while the masses flow past. Sometimes one may stay on a while after all the others have gone by but eventually he too moves off after the herds.

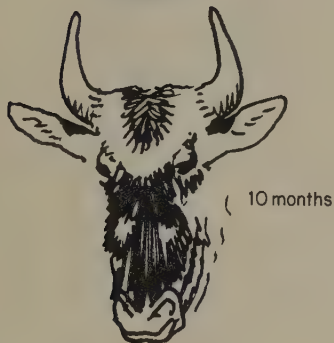
At the time of the rut numerous fights can be observed with both males down on their knees, sliding about in all directions with their foreheads flat against the ground, bosses crashing, and the horns hooking to catch the opponent off balance, a feat made difficult by the lowered centre of balance and the virtual blindness of the competitors while their heads are down. Ritualization of fighting has evidently gone to great lengths in the gnu but the fighting posture, the shape of the horns and the very thick skin on the forehead and throat reduce the risk of damage.



When territories are held for any length of time they soon become recognizable by bare patches made by pawing, horning, head rubbing and rolling. There is always a large pile of trampled dung. The oily secretion of the preorbital gland is rubbed on trees and anthills. The male gnu on his territory will call out with loud grunts at any groups approaching him. This call becomes a chorus whenever herds start moving, particularly during the rut. Watson has noted that there is often a change in the tempo of the bulls' calling in the evening just before the herds move from daytime grazing areas to an adjacent area where the night is spent. As for the cacophony of gnu on the move he suggests the sound helps to create the pervading social atmosphere which is associated with the migration.

Females make a soft cow-like call to their young, which also have a contact-distress call like that of a lost calf. Estes has pointed out that the southern gnu populations are less vociferous than the Serengeti *C. t. albojubatus* and that the timbre is more metallic and can be rendered as "kwank". Other sounds are an alarm sneeze and a deep snort, which is associated with aggressive incidents between adults and young.

In spite of having legs that are short relative to other alcelaphines, the gnu is capable of a fast gallop, which has been described by Dagg (1969) and speeds of 80 kph have been clocked. Alexander (1977) and Alexander *et al.* (1977) have compared the fast locomotion of gnu and hartebeest and the allometry of their limbs.



When on the move gnu string out in long lines, plodding after one another with their heads held low. This posture may be related to their smelling of the track, for the hooves have glands containing a strong-smelling tarry secretion which probably scents their path.

Gnu rest during the heat of the day and feed during the mornings and afternoons. They are often active at night and during the rut are noisy on moonlit nights. They bed down strung out in "strands" and do not normally adopt any protective formation against predators except that the calves lie close to the mothers, which are usually in a group together.

The social structure of gnu herds is highly variable. Talbot and Talbot (1963b) estimated a sex ratio on the Serengeti balanced slightly in favour of the males. Estes (1969) estimated two males to three females in Ngorongoro and Peterson and Casebeer (1972) one male to two females on the Athi-Kapiti plains. Most females calve once every year but Watson (1967) reckoned that the Ngorongoro population is more fecund than the Serengeti one, primarily, he thought, because females breed at a younger age. In many habitats it would seem that something in the region of 15% of the young survive to become breeding adults. The number of adults dying in the course of any one year varies enormously. For example, Watson calculated that the adult mortality rate on Serengeti ranged from 4.2% (1962—1963) to 15.7% in 1965—66 and there can be little doubt that much higher levels are reached in some years. In several undisturbed areas with resident populations, i.e. Kirawira, Loliondo and Mara, gnu seem to maintain their numbers at a stable level. In the Narok area, Talbot (1963b) estimated the population was declining and Foster and McLaughlin (1968) showed a local decline between 1961 and 1967 in the Nairobi National Park. Before the 1961 drought there were very extensive areas of heavily grazed short grass. After a high proportion of the grazers had died off the grass grew taller and this has subsequently favoured the hartebeest rather than the gnu (Stanley-Price, 1974).

In contrast, the Serengeti migratory population has been increasing over a period of about 15 years. Pearsall estimated 101,000 gnu in 1957. Talbot and Stewart (1964) counted over 220,000 in 1961, Watson (1967, 1969) counted 322,000 in 1963 and 400,000 in 1967 and Kruuk (1972) gave an estimate of 500,000 for 1970. A count in 1971 revealed 754,000 and in 1972 840,000 animals (Norton Griffiths, 1973). By 1977 there were 1.3 million. The absence of any major epidemic is thought to be a major factor in this increase.

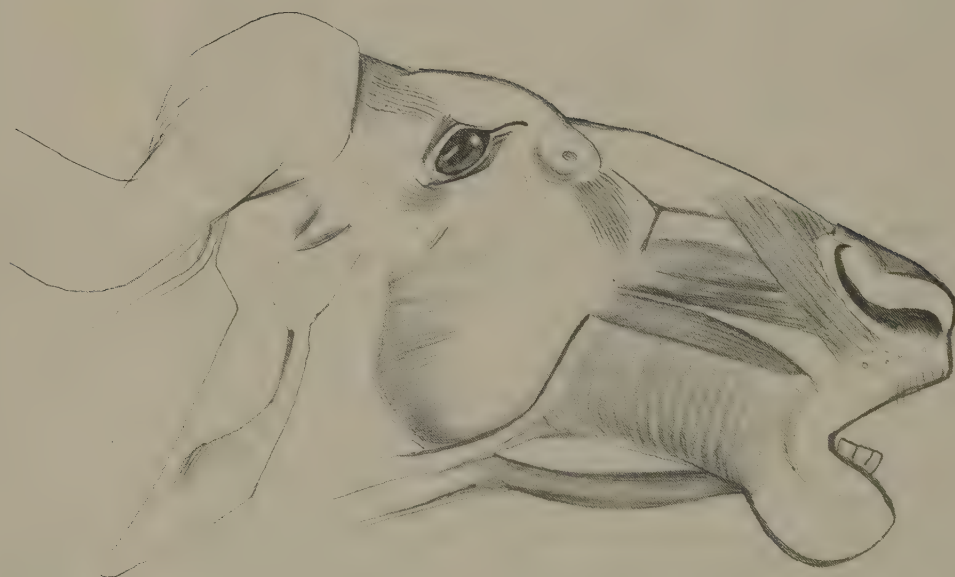
In such highly volatile populations, their age structure, sex ratio and density are obviously extremely variable. In the Serengeti, single concentrations numbering 10,000—20,000 animals are not uncommon, although most aggregations are smaller. In spite of these large numbers, basic social units are often recognizable within the mass. Females with their young of the year are broken up into fairly cohesive, densely packed nursery groups. Up to half the male population are in unstable groups with a more open spacing than the females. This bachelor class is augmented during the birth season by the yearlings when they are expelled by their mothers and territorial males. It is depleted two or three months later as many older animals join the third class, the territorial males.

Estes (1969) believed the females might form their own attachments at the time of calving, when they form aggregations but these associations tend to break down as the calves are weaned and the herds are constantly scattering and reforming in response to the exigencies of the long dry season. The bachelor herds are generally loosely organized but very interesting behaviour was seen during an immobilization operation in a South African nature reserve when two gnu supported a young anaesthetized male by standing on either side of him. When he finally collapsed, they tried to keep him upright by pushing their horns under his shoulder. This implies a level of social co-operation approaching buffalo or zebra but the incident appears to be atypical. The intensity of territorial behaviour wanes considerably after the rut and may become so attenuated that it scarcely exists in the migratory population. It seems that the dry season forces animals to trek longer and longer distances for water. Once out of their territories the bulls' antagonism for other males seems to become easily overlain by sociable impulses and "drinking parties" or even grazing parties of absentee territorials were observed by Estes, who called them temporary bachelors.

In Serengeti, the rut coincides with migration. In the space of 15 minutes Estes watched very large aggregations broken up into hundreds of "wards" (averaging about 16 heads), each in the charge of a single bull. In these conditions, the distances between bulls can be anywhere between 1 and 8 m. Outside the aggregations, the spacing of territorial males depends on the season (Estes reckoned 120—145 m between males during the rut and 130—160 m a month before it) and on the nature of the habitat, with males half a kilometre or more apart in unsuitable country. Above all, the density of male territories depends on the presence of numerous females. Estes noted that when concentrations of females formed on seasonal pastures in the Ngorongoro crater, males from outlying territories came in and sought to establish themselves as close as they could to the mass. The resultant intensification of the territorial network would soon break up after the herds moved on, showing that there are fundamental similarities in the territorial behaviour of migratory and resident gnu populations.

The rains falling after the long dry season signal a sudden revival of territorial activity and Estes noticed that bulls of about 34 months of age left the bachelor herds to take up territories at this time. The extent to which physical condition influences the gnu's territorialism is not very clear. Territorial males continue to graze and thus can keep up their condition during the rut. On the other hand, Estes noticed that they lose condition during the dry season, probably because they do not keep up with the movement after fresh grass. Possibly territories change owners most frequently at the beginning of the rains. Estes noted 54% of his resident territorial bulls still in possession after two years. A marked migratory bull in the Kruger Park returned to its original stamp after six months and Moss (1975) has reported a known male in the Masai Mara reserve that occupied the same territory for 13 years. (On the basis of tooth growth patterns, Watson estimated that a few males live up to 24 years and females to 19.)

The territorial gnu, like other alcelaphines, advertises his status by his erect posture and runs to meet intruders with a rocking canter. The head is held low and nodded in threat while the tail is lashed and the animal



grunts. If any intruding male still stands his ground, the territory holder will often turn or leap sideways and present himself broadside. The challenge ritual follows a similar pattern to that of other alcelaphines but has some features unique to the gnu. For one thing, male gnu sample one another's urine and make the lip curl, *flehmen*, which other alcelaphines have never been seen to do. Sometimes animals standing head to tail rub each other's rump. When pawing and horning they will often roll over on their backs and then return to their horning. A horse-like gesture is a rapid sweep of the long tail towards the head, which tosses sideways as if to evade insects; Estes suggested that this movement implies a strongly ambivalent reaction. The most conspicuous of all displays is the gnu's cavorting, which is readily seen by anyone walking through the gnu's habitat, because the disruption causes a succession of invasions by fleeing territorials and each provokes a running challenge (see p. 451). Cavorting is also a very strong piece of self-advertisement by the gnu in his territory directed towards a neighbour. Estes has described two territorial bulls displaying and explained how dual motivation causes the twisting movements so characteristic of this display:



"Two bulls race besides each other along their (presumed) common boundary and apparently neither dares cross the line and start a fight. What is most remarkable in this performance is that while their heads and forequarters are turned towards one another as though to meet head-on, their hindquarters carry them in the other direction. The result is that they maintain a safe distance apart."

The territorial bull has often been described as an alert sentinel but in fact, territorials are usually more sensitive to other gnu than predators. That this is so seems to be corroborated by Schaller's study on lions in Serengeti, where he found 129 male gnu killed and only 64 females, but Schaller does remark that the sex ratios of killed gnu in other localities seem to be more balanced. A similar discrepancy between hyaena kills has been observed by Kruuk (1972), who found 1.84 males to one female on Serengeti but equal ratios in Ngorongoro. There does, therefore, seem to be something about the migratory Serengeti bulls that renders them more vulnerable. Perhaps it is because their temporary territories are set up quite indiscriminately in little known country. In terms of the lions' preferred prey, the gnu is of ideal size and in Serengeti provides 20—25% of the lions' annual diet (Schaller, 1972b). The proportion would probably be a lot higher if territorial lions actually followed the gnu's migrations.

Because hyaenas are more numerous and more widely dispersed through the gnu's habitat than lions they are probably even more of an influence on the gnu populations. This is certainly so in Ngorongoro, where Kruuk has estimated that hyaenas kill 11% of the gnu population every year, by feeding almost exclusively on calves during the birth season and killing about three-quarters of the year's crop. Since old animals are also killed by hyaenas, there is a faster turnover of population in the crater than on Serengeti, where a disproportionately high proportion of yearlings is killed, probably because of their susceptibility to disease at this age. Kruuk calculated that between 1.6 to 2.6% of the Serengeti population was taken by



hyaenas in a year. Predation by hyaenas and lions alters the age structure in the two localities studied by Kruuk (1972) and Schaller (1972b). The figures for hyaena kills where the ages were recorded reflect both the relative vulnerability of the gnu and the differing age structures.

AGE CLASSES OF GNU KILLED BY HYAENAS
(after Kruuk, 1972)

Age	Serengeti	Ngorongoro
0—12 months	36%	60%
13—24 months	14%	2%
over 24 months	50%	38%

Lions stalk or ambush their prey and unlike hyaenas and hunting dogs give little evidence of selecting inferior animals. Occasionally the gnu are stampeded into swamps or rivers and as many as 64 gnu have been found drowned together as a result. Once caught by a predator, a gnu seldom puts up much fight. It stands or lies moaning and looks "less like the victim than the witness of its own execution" (Estes and Goddard, 1967).

Both wild dogs and hyaenas run adult gnu down in a chase that may cover five kilometres; nearly half of the hyaena chases watched by Kruuk ended in a kill and the gnu that evaded capture outpaced the hyaenas, got into large herds or were left alone after crossing the boundaries of another hyaena clan range. When gnu took refuge in water, they were either killed there by the hyaenas or drowned. However, hunting dogs seldom enter water after their prey. Hyaenas generally rush gnu calves; mothers defending their young often manage to deter a single hyaena but the effort is useless when several hyaenas or wild dogs are involved. In fact, the predators



sometimes attack and kill the mother as well in these circumstances. Very occasionally gnu bunch with the young inside a circle. I have seen this being done against wild dogs; each rush by a dog was met with lowered horns or a short rush. Predation by lions, hyaenas and hunting dogs is continuous and heavy in nearly all areas where there are concentrations of gnu and for all these predators gnu are an important staple. Leopards and cheetah also kill gnu, but usually choose subadult or young animals, as the adults are too heavy and strong for single-handed killing. In Serengeti, lions and hyaenas increased when the gnu increased (wild dogs instead are thought to have declined). The gnus' numbers and movements not only influence predator populations. As the dominant species their grazing alters the food supplies of other grazers and ultimately determines how the rest of the large mammal community in the Serengeti eco-system is interlinked (Sinclair and Norton-Griffiths, 1979). The origins of the gnus' increase lie in an immunization campaign against rinderpest in cattle which was begun in 1952. The well-sustained efforts of the Tanzania and Kenya veterinary departments eventually protected all the Serengeti ruminants from reinfection from cattle. Thus the control of a single disease attacking a single key species has had profound effects at all levels of the Serengeti eco-system.

Disease is an important controlling factor for all gnu populations, the principal danger being rinderpest or "yearling disease" which is most frequently contracted by animals in their first year. This disease tends to manifest itself when the animals are feeding on new green growth after a long dry spell, hence the timing of the last major outbreak in 1961 (Taylor and Watson, 1967). These authors have shown that rinderpest is not enzootic in the wild animals of the Serengeti region but that the settled areas of Loliondo became a reservoir for this disease. In some areas the Masai have kept their cattle away from gnu during their calving period to avoid infection with malignant catarrh, which is endemic in gnu. Antibodies for *Brucellus abortus* are also present in gnu (Watson, 1969).

The larvae of *Gedoelestica* and *oestrus* flies live in the nasal passages and pneumatic cavities of gnu and have been reported to get into the brain occasionally. Anthrax has been diagnosed in gnu and sarcoptic mange is common; they also suffer from hoof gangrene. There are various endo- and ecto-parasites (see Appendix III). During a huge die-off during a drought in Botswana, Child (1972) found that more young calves and old females died than any other class. Talbot and Talbot (1963b) attempted a break-down of mortality factors and estimated that disease accounted for 47% of the deaths in the Narok area, whereas 37% were due to predation and 16% to accident. Obviously the patterns will vary greatly from year to year and from locality to locality.

Some of the smaller animals on the plains have made special accommodations to the vast herds of gnu. For instance, crowned lapwings, which are very numerous on Serengeti protect their nests and young by making a wing display whenever an animal shows signs of trampling them (this is also directed at an oncoming vehicle). This bird behaviour has probably derived from an intraspecific display but it must have acquired a selective advantage as gnu and zebra avoid a bird in this posture.

Although some courting and mating continues for much of the year, most sexual activity takes place, as has already been noted, during the period of the migration. The moving herds of females and young pass through temporary male territories and are herded into units averaging about 25—30 animals. Watson (1969) terms these "pseudo herds" in "pseudo territories". The more elaborate territorial behaviour is abbreviated or absent but the bulls are extremely active and pugnacious.

Cows in oestrus may pass through the stewardship of several bulls and are mated by each of them. Bulls approach oestrous cows with the chin extended and the neck and ears somewhat lowered. They often foam at the mouth; mounting is accomplished very rapidly and the male arches his neck and rests his chin on the female's back.

Gestation is about 240 days and the births are very closely synchronized, with about 80% of the Serengeti population born within three weeks (Watson, 1969).

The newborn gnu can stand up and can run within five minutes. Mothers care for only their own young and as the calves are easily lost in the course of the herd's mass movements the mortality is enormous; Talbot and Talbot (1963b) thought this constituted a mechanism for natural regulation operating through herd size but the subsequent growth of numbers in the migratory population has revealed that the overall effect on numbers is probably negligible.

Calves form small groups together and engage in butting, chasing and "stotting". They first start grazing at the age of ten days. Maturation rates vary, females first conceiving anywhere between one-and-a-half and two-and-a-half years old. Males, instead, become sexually active when over five years old.

Sustained yield cropping of gnu has already started in East Africa. Peterson and Casebeer (1972) have recommended a safe annual harvest of 6% with 9—14% cull possible if constantly monitored; more males than females should be taken and November—December is the best time for

cropping. The effect of fencing on wild populations can be drastic and Ebedes (in Estes, 1969) pointed out that control fencing in Botswana and South-west Africa has cut large herds off from water and reduced the gnu population from at least a quarter of a million to some 30,000 in a few years.

In some parts of Masailand gnu used to be captured as calves and run with the cattle. Hinde and Hinde (1901) reported that lactating captives were used to feed cattle calves and thus save more cow's milk for human consumption but it is unlikely that this was a common or very successful practice. Gnu have been domesticated in many zoos and ranches. However, they compete with cattle and Kettlitz (1962a) has reported that numbers are decreasing on Transvaal farms and some ranchers are in favour of exterminating gnu because of competition and disease. Similar attitudes prevail among some veterinary officers and farmers in East Africa and the animal is unlikely to be a popular animal on farms and ranches.





Horse-like Antelopes, Hippotragines

Hippotragini

Genera and species

Hippotragus equinus

Hippotragus niger

Oryx gazella

The larger species of African antelopes can in every case have their genealogies traced back to much smaller and less specialized species, either through fossils or by reference to surviving relatives. The duikers, tragelaphines, reduncines and alcelaphines are adaptive arrays, each with a wide variety of types and sizes, some of which are abundantly documented in the fossil record.

The hippotragines are instead represented by five African species and a sixth in Arabia. Four of these are desert or near-desert species and the morphology of the few African fossils that have been found suggest that the tropical roan and sable antelopes have a common ancestry with the desert-adapted oryx.

The implication that these two species derive from an arid-adapted invader from northern Africa and southern Eurasia tends to be borne out by their isolated position in the spectrum of tropical antelopes and by similarities in size and build between Pliocene and living hippotragines.

What are their origins? This question has generated much controversy and led to a variety of taxonomic allocations vis-à-vis the other African antelopes. The various nomenclatures were reviewed by Simpson (1945), who tentatively grouped the Hippotragini with the Alcelaphini and Reduncini but admitted that this subfamily was "not surely natural". Ansell (1968) followed this arrangement but added *Pelea* and *Ammodorcas* as monospecific tribes. In the most recent arrangement Gentry (1978a) reduced the association to Hippotragini and Reduncini but added that he thought the late Pliocene *Hippotragus bohlini* had features compatible with descent from the Boselaphini.

The tendency to ally Hippotragini with Bovini or Reduncini has been due to a reliance on teeth as the ultimate taxonomic criterion. In each of these groups the molars are broad and reinforced by basal pillars but I consider that each of the three groups has acquired a broadened molar battery quite independently. Basal pillars are simply extra folds of enamel forming in between the two molar columns (protocone and hypocone) thus packing out the deep trough on the lingual surface. In the primitive bovid tooththrow the masticatory function of a succession of deep valleys between each tooth and between each pair of cusps is to provide blades against which the very narrow edges of the lower molars can slice. The action is analogous

to repeated cutting with a saw-toothed pair of scissors. This type of mastication is effective for slicing up relatively small quantities of food and is probably adequate for larger intakes that are rich in nutrients and not too hard (such as the typical tragelaphine diet).

In all major bovid lineages the earlier species were relatively small and all of them started with relatively sharp-cusped molars by which mastication was performed with a similar slicing action. Almost all of the smaller-sized bovids chew in this way and retain this type of tooththrow today.

The mechanism becomes less efficient when greater quantities of poorer quality food are eaten and there are several reasons for this. As consumption is increased a point is reached when the number of cutting edges needs to be increased. Larger mouthfuls are better milled than sliced and harder foods require greater power to the bite, which puts more strain on the tooth and speeds up wear.

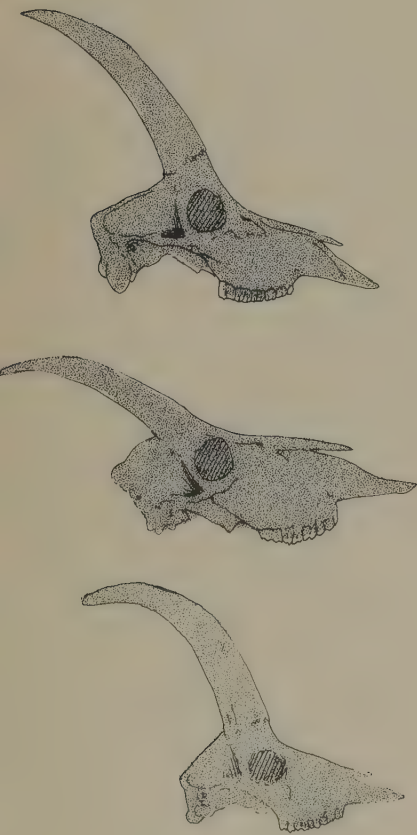
These pressures on dentition are met in each of the bovid lineages that increased body-size and tackled more difficult diets. In spite of some variation in proportions, the structural similarity of most small bovid tooththrows has ensured that the development of mill-like teeth has followed a similar pattern in Bovini and Hippotragini.

These dental similarities do not imply close relationship. Rudimentary cusplets of enamel can be found on the lingual surfaces of molars in giraffes, tragelaphines and duikers as well as in bovines, reduncines and some early fossil caprids.

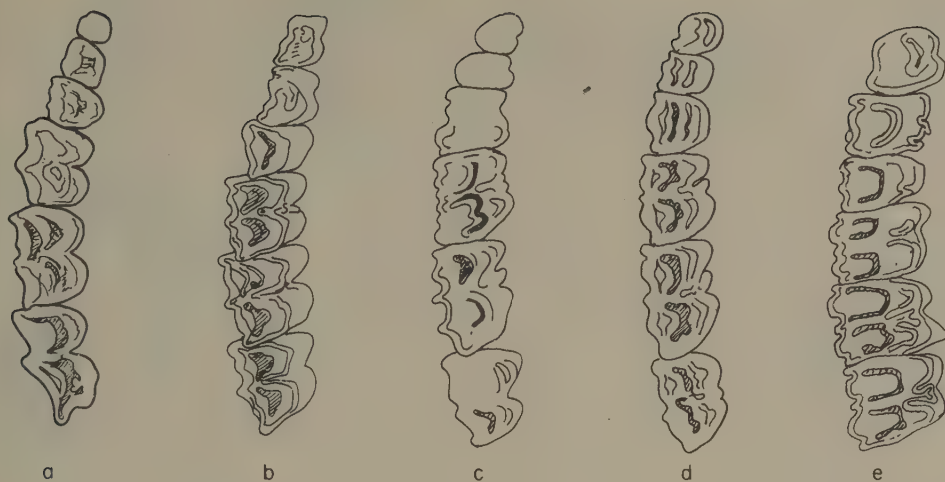
As Simpson (1945) pointed out, it is difficult to draw a sharp line between caprines and antelopines, but the former are unequivocally Eurasian, having evolved within that immense area of mountain belts that runs from the European Alps to the Pacific.

In the Pliocene of the Siwalik Hills and Samos there are large numbers of fossil bovids, some of which possess budding enamel pillars and most of which have a mixture of hippotragine and caprine features. The larger ones such as *Palaeoryx pallasi*, *P. major* and *Protoryx longipes* tend towards the former while the smaller such as *Microtragus* and *Pseudotragus* are more like goats. Considering the extensive range, the considerable variety, success and above all, the age of the caprines it would be somewhat surprising if they had not evolved large forms. It must be recognized, however, that increased scale is capable of initiating anatomical and ecological changes that may so transform morphology as to utterly disguise an otherwise close relationship. I believe this is what has occurred and I consider that hippotragines emerged in Eurasia as the larger-scale, open-country branch of an early caprine lineage, modifying their teeth and elaborating their horns in ways that were different from their smaller mountain-dwelling cousins. The larger members of this radiation seem to have disappeared early in the Pleistocene, perhaps a smaller choice of habitats in Eurasia combined with keen competition from equines and advanced bovines eliminated them.

Notwithstanding differences in period, provenance, body size and tooth structure there remain some striking resemblances in general conformation of the skull between some Pliocene fossils (such as *Protoryx carolinae*), the living *Hippotragus equinus* and relict caprines such as the Rocky Mountain goat, *Oreamnos* (see margin).



Top: *Hippotragus equinus*.
Middle: *Oreamnos americanus*.
Bottom: *Protoryx crassicornis*.



Toothrows from left to right:
a. *Antidorcas bondi* (a Pliocene antelope); b. *Protoryx carolinae* (a Pliocene caprine); c. *Sivoryx cautleyi* (a Plio-Pleistocene hippotragine); d. *Oryx dammah* (the scimitar horned oryx); e. *Hippotragus equinus* (the roan antelope).

The currently known later Pliocene fossils in which caprine-hippotragine relationships are evident date from a period after their actual divergence, which might have been early in the Miocene. Even within the Hippotragini, *Oryx* and *Hippotragus* lineages were recognizably distinct by the late Pliocene (Gentry, 1978a).

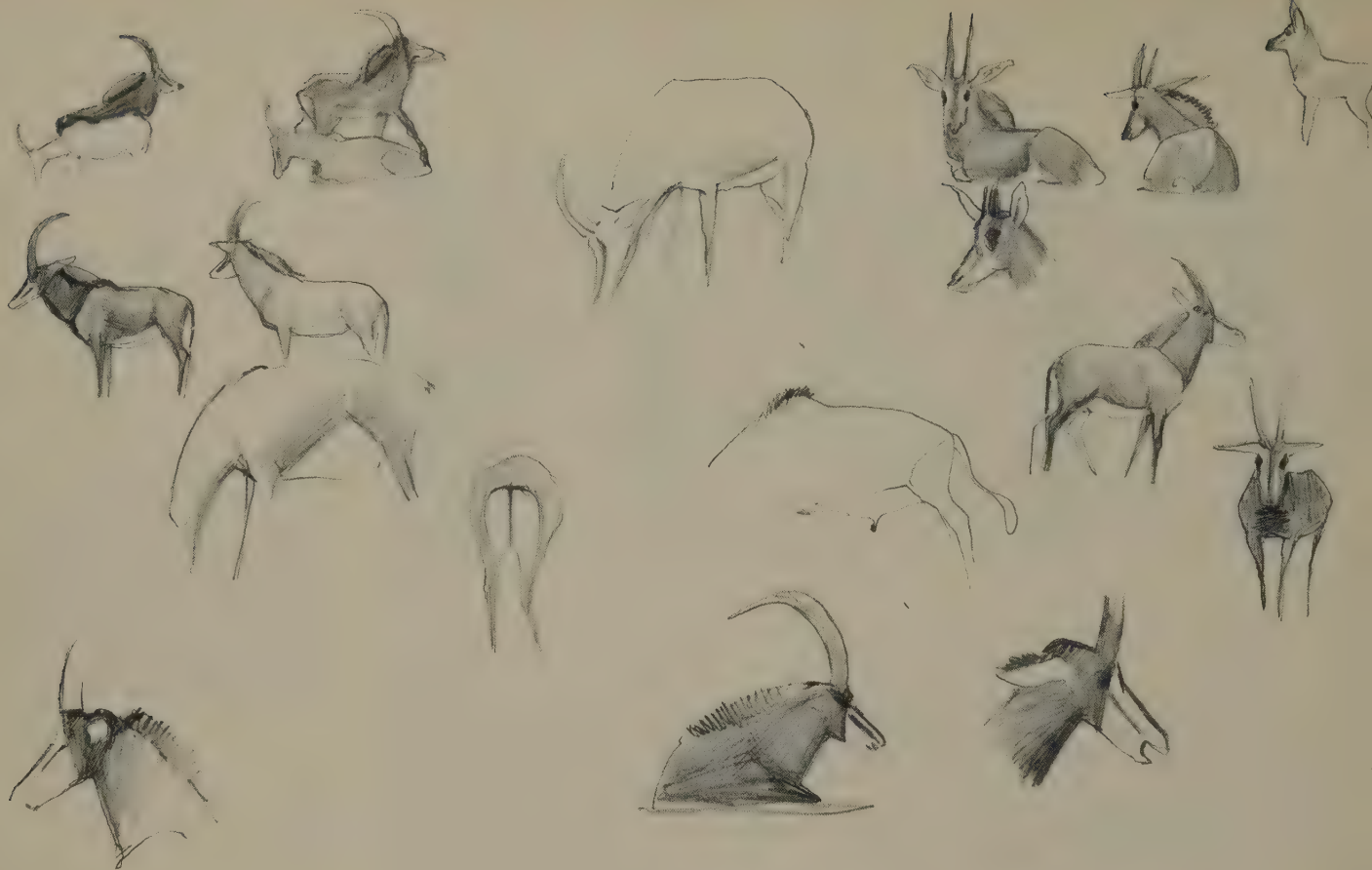
Hippotragus have high narrow skulls whereas *Oryx* have lower, wider skulls, differences which are influenced by the depth of the jaw and by the rooting and direction of the horns. The latter formations reflect different fighting techniques (see pp. 28, 168).

In spite of the early divergence of these genera an understanding of both their ecological advantage and their limitations can probably be usefully informed by an awareness of dry-country origins and their adaptation to heat, drought and coarse foods. Their anatomy, ecological dispersal pattern, modes of communication and social structure may all have been conditioned by an ancestral "desert ordeal", even where the contemporary species lives easy and has come to depend on frequent watering.

The fact that no other bovid group has been able to challenge the Hippotragini for the larger-scale desert bovid niches implies that they have had a long head start in adapting to heat-stress, drought and the very variable quantity and quality of arid land pastures. This is consistent with derivation from the Caprini, in as much as the latter emerged at a very early date (more than one African species was recognized by Gentry (1970a) in the fourteen-million-year-old Fort Ternan deposit).

Not only is a caprine relationship implicit in positive adaptations but, in common with other long-established groups they appear to share some peculiar limitations which may provide some insight for our consideration of the evolution of hippotragines and help further define their ecological roles.

In proposing a "desert ordeal" it is not necessary to assume that the common hippotragine ancestry was as specialized as the modern oryx. Capacity to withstand heat and drought has probably been greatly enhanced in *Oryx* and *Addax* during the several million years of their existence as



distinct genera, but the foundations for this tolerance must have been provided by a stock with physiological abilities that were already exceptional.

Ancestral *Hippotragus* must also have begun with more modest but nonetheless decisive advantages, comparable perhaps with those of many modern Caprini. Specialization in mountainous or arid areas apart, contemporary caprines typically belong to ecological communities where there are relatively few other herbivores (Schaller, 1977). That their parental stock was formerly more ubiquitous and less specialized is implicit in an abundance of fossil species in the early Eurasian Pliocene. For example, none of these had the short metapodials of modern goats (Gentry, 1968).

Both caprines and hippotragines occupy constricted niches today. Varied tooth structure in both fossil and living forms can be correlated with some dietary diversification (sheep are grazers, goats browsers) but the majority of Caprini and Hippotragini are broad-spectrum feeders and there is little evidence that they are severely constrained by diet. Hippotragines resemble caprines in being limited to habitats or localities where there are fewer species and lower numbers of other herbivores but this situation does not seem to be a product of direct competition for food. They are often described as having "narrow habitat preferences", yet the habitats in which hippotragines have been recorded are very varied and low densities of other herbivores are a more consistent feature of their distribution than physical and botanical characteristics (see p. 546).

Rigours of the environment are often sufficient to explain why Oryx find themselves in areas with few other herbivores, but why should roan and sable antelopes, sharing areas of fairly high rainfall and primary productivity with a wide range of other antelopes, be limited to small localities or discontinuous vegetation belts in which the density of herbivores is markedly lower than in neighbouring areas?

Is this "preference" conditioned by a positive avoidance of other herbivores? This does not seem to be the prime reason because neighbouring areas that are periodically vacated by other herbivores are not automatically attractive even if there is grazing there. Instead the proximate factor seems to be a strict adherence to traditional refuges and circuits. Very conservative home range patterns have been observed in oryx, sable and roan antelopes. In *H. equinus* Joubert (1974) identified the interdigital gland secretions, dung and horned vegetation as the marks of a herd's activity within its home range and he pointed out that these marks may inhibit strangers from intruding into the "activity zone" of a herd which maintains a more or less closed membership. The disadvantage suffered by an intruding animal or group of animals is therefore exactly analogous to the disadvantage of intruding individuals of primitive territorial species such as *Neotragus* or *Madoqua*. Likewise, the advantages of possessing a well-known activity zone are analogous to those of solitary territorial species but the entity is no longer an individual or a pair but a "reproductive unit" or clan of related and hierarchically organized females with their young. In oryx a number of males may be present for a large part of the year. In the roan antelope a single, mobile, intolerant male accompanies the herd. Sable herds, instead, range over one or several territories held by mature resident males. Thus there is a distinct gradient in social structure.

Considering that areas suitable for roan were very limited in his study area (the Kruger Park), Joubert (1974) explained small, scattered herds as the product of a population-regulating mechanism operating through the mutual intolerance of the herds to match the animals to the carrying capacity of their habitat. Joubert thought that carrying capacity was determined by the physiognomy and quality of the vegetation and by an optimal social spacing for the species.

There seems to be little doubt that a major proximate factor restricting the reproductive units of roan and other hippotragine antelopes to particular areas is their reluctance to leave traditional activity zones or circuits. (In Tanzania I know of one locality which the oral history of the local people claims to have been occupied by roan antelope for as long as people have been settled in the region, a period in excess of one hundred years).

It is unlikely, however, that either roan or sable antelopes are normally directly limited by their food supply. Less efficient feeding strategies could perhaps marginally influence the status of these antelopes in a local grazing community but I think it is more likely that their low numbers relative to other generalized herbivores can be attributed directly to higher mortality rates which in turn are probably a legacy of early adaptation to relatively sparse resources.

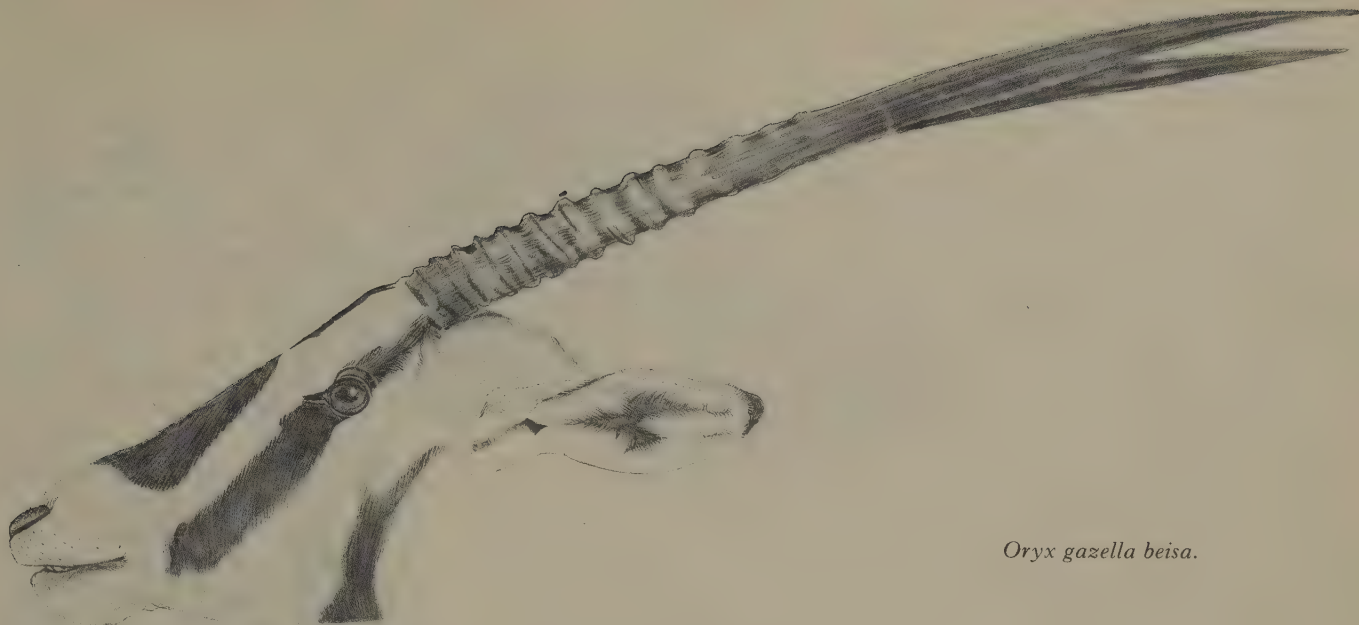
Oryx and many caprines belong to very small herbivore communities because deserts and mountains have limited resources. Very few herbivore species scattered in difficult habitats means smaller numbers of predator species at proportionately lower densities. Therefore a corollary of adaptation to a sparse resource base is fewer predators of fewer species.

The phylogenetic dimension of this is that when arid-adapted antelopes of Eurasian or North African origin moved into richer vegetation belts they encountered higher levels of predation. Not only are predators more varied and numerous but, as I have already pointed out, carnivores have been continually "updated" as they have to keep up with evolutionary changes in their prey (Vol. IIIA, p. 3). Hippotragines have unusually vulnerable young and may become exceptionally susceptible to predation at various stages of their life cycle as a direct result of their evolutionary history. The details of this vulnerability remain to be documented but the broad pattern seems to be clear, even on the incomplete evidence now available.

LION PREDATION OF *HIPPOTRAGUS* SPECIES IN KRUGER PARK (from Pienaar 1969a)

Species	Relative abundance in prey community	Relative frequency in all lion kills	Lions' preference rating	Percentage killed by lions (of total predation)
Sable	0.58%	1.52%	2.62	93.3%
Roan	0.16%	0.26%	1.62	88.7%

Predator-prey relationships studied by Pienaar (1969a) in the Kruger Park showed that both roan and sable antelopes were highly susceptible to lions even when their numbers were extremely low. Pienaar expressed

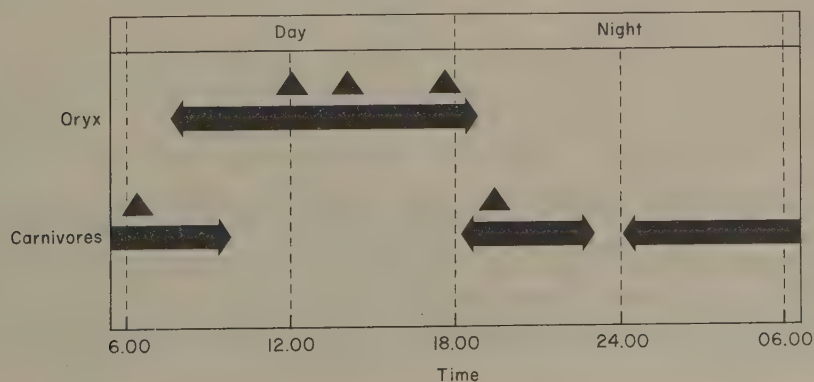


Oryx gazella beisa.

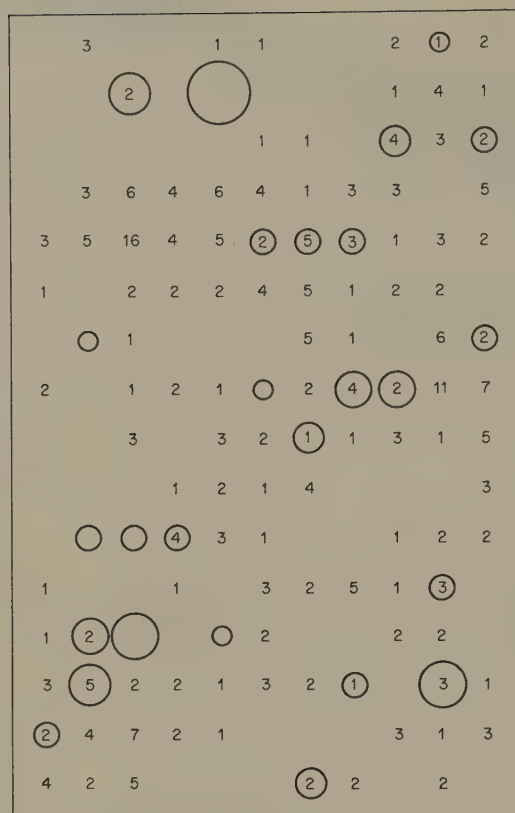
such susceptibility in terms of the lions' "preference ratings", which were a ratio between the percentage of recorded lion kills and the relative frequency or abundance of the prey species. The ratios showed that the sable was killed by lions more than two-and-a-half times as frequently as its abundance merited and the roan over one-and-a-half times.

The hippotragine's restriction to limited localities does not seem to be the result of a "narrow habitat preference" or a deliberate avoidance of other herbivores (although there may be an element of this). Rather it is the product of two interacting forces. One is long-term suppression or elimination in high density areas because of the selective preference for hippotragines by more numerous predators. The other is a conservative land-tenure pattern which is reminiscent of the equally persistent territorialism of gazelles and neotragines. This serves to attach a population nucleus to areas or vegetation complexes where trial and error over generations has proved that predation is at levels that they can withstand and where the topography of the home range is well known.

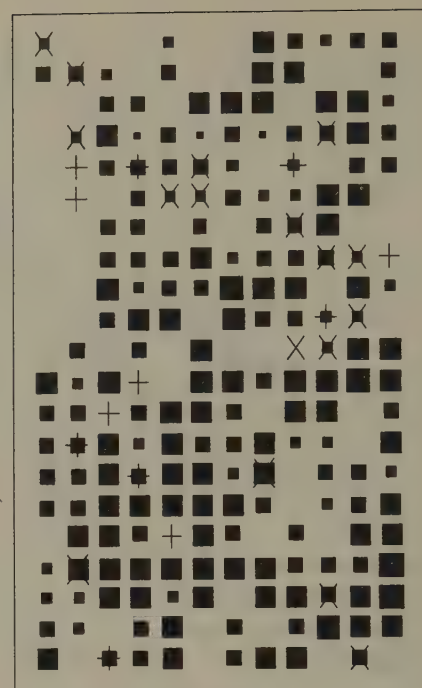
The activity pattern of hippotragines might also have been modified by predator pressure. Waterholes are a common hunting ground for lions and hippotragines are not the only antelopes to show extreme caution in their approach. Ayeni (1975) timed the visits of animals to waterholes in the Tsavo National Park and found virtually no overlap in the main visiting times of *Oryx* and the large predators. The respective peak periods of visiting were well separated (see below).



Dry-season visits to artificial waterholes in Tsavo National Park, showing temporal separation between oryx and carnivores. Arrows indicate peak of visits (from Ayeni, 1975).



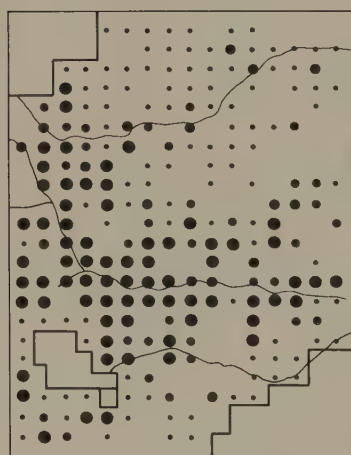
0 50 km
○ Relative abundance



0 50 km

kg per sq. km
■ 1-10
■ 10-100
■ 100-1000
■ 1000-9999
■ 10000+

× Wet season distribution
+ Dry season distribution



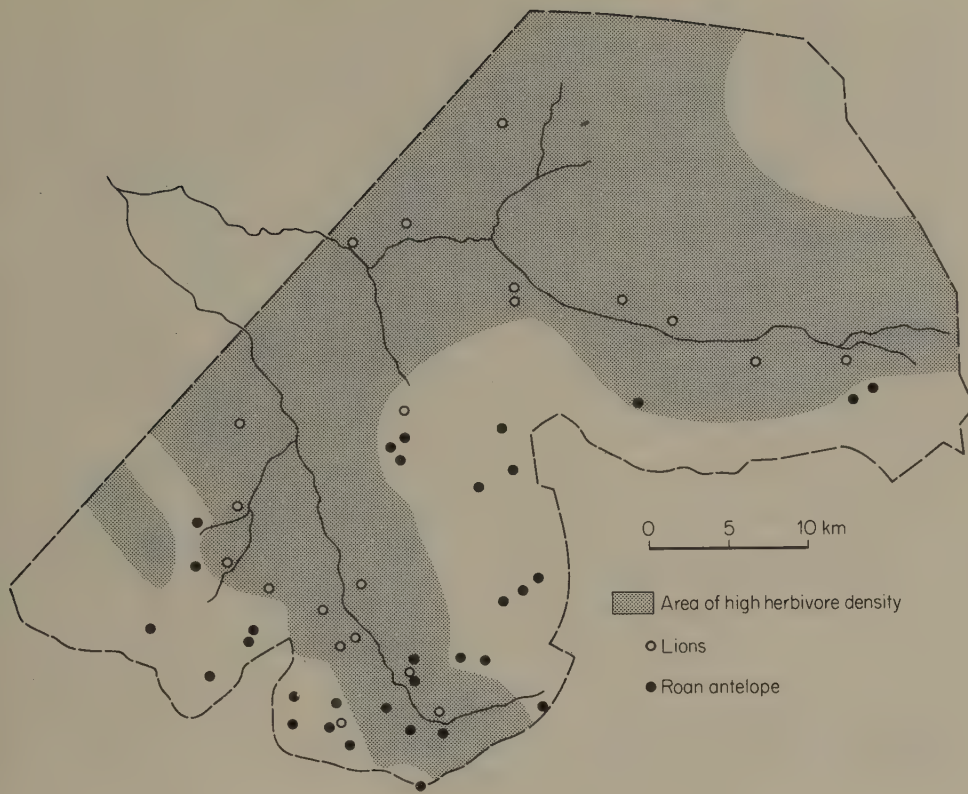
km²
• 0.1-0.99
• 1.0-9.99
• 10-99.99
• 100-999.9

~ Rivers



• kg per sq km

Top left: distribution of sable in relation to the number of other large herbivore groups recorded in 10 km squares during an aerial survey of North Rukwa district (Ecosystems, 1978). Top right: distribution of roan antelope in North-east Jonglei province in the wet season in relation to total biomass at that time (Metif-Babtie, 1980). Bottom left: distribution of wildlife biomass (as kg per sq. km) in North-east Tsavo during September 1974 (a typical dry season month) contrasted with (bottom right): dry season distribution of oryx (as numbers per sq. km) (Cobb 1976). Although these figures are not directly comparable the overall pattern is suggestive.



Map of Kidepo National Park showing area of high herbivore density with records of lions and roan antelope over 23 months. (Data from I. Ross.)

The maps opposite show b) a small-scale distribution pattern for roan antelopes in relation to total herbivore biomass (and above, a larger scale plot of roan sightings over 18 months in relation to the distribution of other herbivores and lion sightings), a) sable antelope distribution in relation to other herbivore groups and c) dry season distribution of oryx compared with the overall biomass of herbivores during a representative month in Tsavo National Park. The number or biomass of other herbivores can generally be taken as a very rough index of predator pressure, and in the case of the sable's *miombo* habitat there is the well-known aversion of hyaenas for this vegetation type (see Vol. IIIA). Having adapted to a difficult and fluctuating habitat, sable antelope can sometimes sustain relatively large numbers and artificial protection in the Shimba Hills has led to a steady population increase during the 1970s. Conversely, in 1953 I had the opportunity to observe persistent and concentrated predation by lions on an unusually large aggregation of sable antelopes in the Issawa River area, three or four animals being killed each week over a period of several months.

An exceptionally high rate of juvenile mortality makes it unlikely that long horns are normally of much use as a defence against predation. Hippotragines aggregate readily on a temporary basis but social units generally number less than 20 animals and tend to have closed membership. Horns provide female members with the means of excluding outsiders from scarce resources. The hierarchies that females establish within these units may also be served by the possession of horns but this does not explain parity in horn length with the males. In the sable antelope there is much greater sexual dimorphism and this can be correlated with a single significant

difference in their social structure. Sable attempt to force females into remaining on their territories. In desert environments any barrier to the females' free movement would tend to prejudice survival and it is appropriate therefore that male oryx, being unable to coerce females, do not attempt to do so. The roan is an intermediate case and its wooded grassland habitats are also somewhat intermediate between those of oryx and sable.

In all hippotragines the sense of sight is pre-eminent. This is reflected in their visual alertness and in their ritualized semaphore of gestures and postures (described and illustrated in the profiles). They have large and active pedal glands which assist scent tracking; facial and inguinal glands are lacking but they have a generalized body odour. All hippotragine species tend to damage vegetation with their horns but there is a gradient in this behaviour which is more frequent in sable bulls and least in oryx. Such visual marks combined with faeces, pedal scent and parading by the bull delineate a male territory in sable. In roan society such signals result in both individuals and separate groups avoiding one another (Joubert, 1974) and, for a male oryx, marks might delineate a temporary territorial focus.

Hippotragines are grazers, preferring young nutritious grasses if they are available but they are able to sustain themselves over the dry season on coarse dry fodder. Their normal cropping pattern resembles that of the zebra, in that the grass tends to be sampled over a fairly wide area without intensive mowing. Sometimes grazing may be conducted on the knees, particularly by the younger animals, which have relatively long legs and short necks.

Hippotragines have unusual stamina and are broad-chested with large hearts and lungs, which give extra breadth to the body. Gaits are sure-footed and long-strided without relying on exceptionally long legs. Their hooves are peculiarly broad and apparently equally well-adapted to sandy and stony soils, but not to marsh. (Some of these characteristics may be a reflexion of common origin with the caprines.) The need to make periodic or seasonal movements varies from species to species and within each species according to the area they inhabit. Desert oryx are thought to move great distances, roan less and sable the least.

Like many other antelopes, the hippotragines produce relatively helpless young which hide for some weeks after birth. These infants have a cryptic natal coat completely unlike that of the adult. Gestation takes about eight or nine months.

In a Shimba Hills sable herd containing 18–29 adult females, Sekulic (1978) has recorded births over a period of four years. There was no seasonal consistency because the calving interval was about nine months, but the synchrony of births within the herd was quite remarkable. Each season's crop of calves not only increased in number but the period within which the births took place narrowed down until 81% of the births were taking place in three months. Birth synchrony correlates with the size of a herd, and three other small herds from the same locality showed much more scatter. The increased precision of synchronized breeding as a herd



Sable antelope, *Hippotragus niger*.

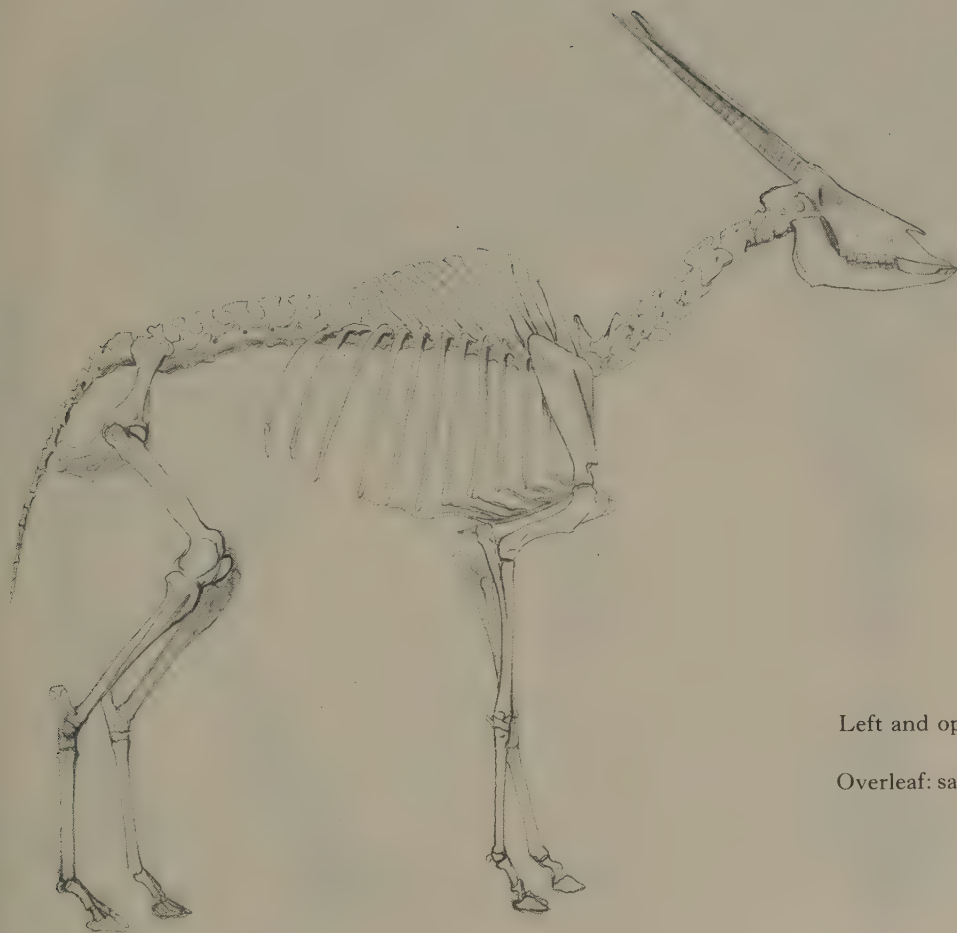
increases its size has several advantages. Individual mothers can spend more time grazing and less on guard and predator detection and defence are improved by several mothers being available. The calves may also benefit after joining the herd by being in a nursery group (Sekulic, 1978).

It is possible that similar mechanisms operate for oryx and roan when adult female numbers in a local "reproductive unit" (Eisenberg, 1977) exceed about 20 but a consistently short birth interval is probably dependent upon optimal feeding and a low level of predation. Both these conditions were met in the Shimba sable because their pasture was subject to management and nearly continuous observation by humans deterred the few predators.

Compared with many alcelaphine and reduncine species the hippotragines seldom realize even a small part of their breeding potential. The success of the Shimba herd is of great interest as an example of a density-dependent reproductive mechanism with innumerable fascinating implications. Sekulic's observations also illustrate how much remains to be learnt about this small tribe of antelopes that survive in ever-diminishing numbers across a wide range of habitats and they illustrate how unexpected results can be achieved by patient and sustained concentration on a known population. Locked up in the intricacies of their biology, shaped by an immigrant ancestry and a complex of advantages and limitations, the hippotragines possess the potentiality for real ecological success. It will require a great deal more study before the prerequisites for a hippotragine's success are understood.



When we view the immense desolation of the Sahara and watch man-made deserts extend everywhere with each passing year it should be remembered that these antelopes once ranged the sands in their hundreds and thousands. Where will we learn how they did it?



Left and opposite: oryx, *Oryx gazella*.

Overleaf: sable antelope, *Hippotragus niger*.







Sable Antelope (Hippotragus niger)

Family Order Local names

Palahala, mbarapi (Kiswahili), Ol-gisauroi
(Masai, Kidorobo), Shambe (Kidigo).

Bovidae
Artiodactyla

Measurements head and body

197—210 cm

height

117—140 cm

ear

16—19 cm

tail

38—46 cm

weight

235 (216—263) kg males

220 (204—232) kg females

horns

50—154 cm

(164 cm in Angola)

Sable Antelope (*Hippotragus niger*)

Race

Hippotragus niger niger (includes *roosevelti* and *kirkii*)

Sable are rotund, barrel-chested antelopes with a short neck and long face. The legs are slender but not very long and the hooves are compact but relatively broad. Both sexes carry scythe-shaped horns which rise from a rather narrow forehead. The ears are long and pointed.

This species changes its colouring with age and this peculiarity is related to a social organization that is very largely based on rank by age. The calf, which must be as inconspicuous as possible, is dun and almost without markings. As it begins to take its place in the herd its coat becomes a rich russet; the belly and haunches become clearly differentiated as do the facial markings. Females then change only very gradually as they increase in age and status; along the margins of their white face and body markings the contrast becomes heightened by a darkening which then flushes over the neck, shoulders and mane. Eventually red becomes limited to rump and hindlegs and in an old cow the forequarters are almost wholly black.

The sequence of colour change is significant for the darkening of neck, cheeks and mane both emboldens the silhouette of this, the threatening end of the body, and also heightens contrast along a line that carries the sweep of the horns straight across the face to the dark neck and shoulders, so that an increasingly geometric configuration is given to the forequarters as a dark conical base to the prominent horns. One effect of this is to give the muzzle a peculiarly detached appearance in profile. Viewed head-on these stripes serve to emphasize the verticality of the horns.

The hierarchically-organized females wander over an extensive area, their overall cohesion depending on the resources of the range. However, at any one time but most particularly during the rut, the local movements of the herd, or of its subgroups, are controlled by the territorial males, which are spaced out at intervals of 1—3 km apart. A male's ascendancy, despite his being an impermanent member of the hierarchy, is ensured by his being slightly larger and decisively more heavily horned and it should be observed that his colouring actually represents the absolute climax of the subtle colour-range which helps grade the seniority of the cows by age.

The visual emphasis of horns, height and shoulder mass is greatest in the form of a mature bull. A bull is unquestionably top of the hierarchy within his own area but territorial status in a favourable and central locality is probably acquired some years after he has turned wholly black. Territorial males may tolerate submissive juniors, even within a breeding herd but I have watched senior cows consistently persecuting partially darkened sub-adult males and I suspect that harassment from females may be as conclusive as persecution by the bull in driving the young males of three to four years of age into temporary bachelorhood and that their colouring



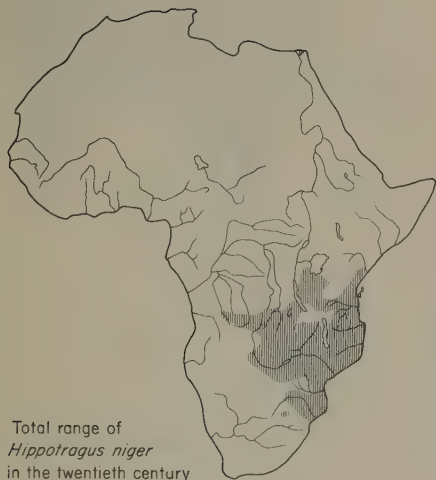
might influence the females' reaction. Whereas young males keep their distance from intolerant seniors, young females disarm aggression by a more intense submission; thus the cohesion of the female group is maintained.

As the young males mature, their physical state can be largely measured by the extent of black colouring and they increasingly avoid contact with one another and become attached to a piece of land, a process that appears to be speeded up during the rut (Grobler, 1974). Being a residential species, these young bulls will normally find territories within the limits of their parent herds' traditional range. Since they may circulate over areas between 13 sq. km (Estes and Estes, 1974) and 320 sq. km (Child and Wilson, 1964), the opportunity to set up territories and the proximity and relationships between males are very variable. Subdominant males may continue to live within the areas of seniors, only retreating when there is a breeding herd; or else established territory holders may be fought and displaced. Alternatively, they may have to settle in country on the peripheries of the herd's normal range.

Within the female herd, a shiny black male sable can be as well described as the superdominant member of the hierarchy as the owner of a territory. However, amongst males there is nothing but horn size, weight, strength and temperament to distinguish one from another. In this context the qualities that enhance close contact dominance are even more impressive in the service of territorial display. Climbing termitaries, debarking the branches of trees with his sharply corrugated horns, pawing the ground before dropping his dung and occasionally kneeling to horn the ground or smash small bushes—these are the regular routines of a male on patrol; and the ultimate definition of a territory's extent is the repeated presence of its owner and his ability to intimidate or fight his neighbours. The sable bull is himself the principal advertisement of territory—an imposing black triangle crowned by great arcs of horns and tricked out with white flashes.

In open habitats such extreme conspicuousness might tend to be both superfluous and dangerous but sable territories are in woodland or include a wooded refuge, where visually based advertisement is somewhat neutralized by the dappling of tree trunks and shadows and predation levels are in any case low. Ungulates that have evolved in heavily wooded country nearly all rely on scent for territorial marking and the sable's very flamboyancy may represent the exaggeration of a mode that was evolved in open country and which betrays the sable as an invader from the plains. In fact, the species is not wholly confined to woodland; indeed it has adapted to live along the woodland-grassland edges, taking advantage of the seasonal grazing mosaic of the *miombo* (*Brachystegia*) woodland belt (see Vol. I, pp. 32–33). Estes and Estes (1974) suggest that the amount of "edge" or ecotone habitat may be at least as important as the actual composition of vegetation in determining the sable's habitat.

The sable populations of eastern and southern Africa have had a more or less continuous distribution until recently and the types from which the subspecies *roosevelti* and *kirkii* were described are not representative of recognizable populations with definite ranges. In Angola, on the other hand,



Total range of
Hippotragus niger
in the twentieth century



there is an isolated population of large-horned giant sables, *H. niger variiani*, which has been the subject of study by Estes.

The *miombo* woodlands are not a uniform habitat and the sable move with the seasons, changes which are determined by their preference for new grass growth and by their need for water during the dry season and firm ground underfoot during the rains, but which might also be influenced by rutting and giving birth. Twenty-eight species of food plants were recorded by Grobler (1974) in Rhodesia but he found sable to select grasses of medium height, and species most commonly eaten throughout the year are *Panicum*, *Heteropogon*, *Eragrostis*, *Themeda* and *Urochloa*.

In the *miombo* woodlands, moist shady conditions alternate with a period of scorched earth after the annual grass fires have burnt off the fine-leaved grasses that sustain the sable during the wet season. These tufted

perennials are the dominant woodland grass *Andropogon*, *Brachiaria*, *Digitaria*, *Panicum* and *Setaria*. Estes (1974) found sables grazed relatively lightly, searching out green clumps to crop by the mouthful rather than selecting small shoots. The woodland grasses grow on well-drained soils which soon dry out after the rains stop. When this happens the sables, which had been dispersed in small groups, begin to gather and move towards the valleys or other localities where the grass is greener. Over this period they may feed in fairly long grass.

After the burns they descend to where the water table is higher and together with other antelopes they tend to concentrate in large aggregations on lawns and fresh growth, mostly fire-climax dominants such as *Themeda* and *Hyparrhenia*. Coarse grasses are avoided except at an early stage of growth. Grazing is supplemented by herbs, legumes and some browse from shrubs and trees but Estes reckoned these never exceed 20% of the diet. The leaves of a dominant woodland tree, *Julbernardia*, are browsed frequently in the early part of the year, when it is wet; whereas the dry heads of *Blepharis bainesi* are eaten in July. Other plants regarded as favourite foods are *Dolichos* and *Mucuna* and the legumes *Lettuca variiani* and *Cryptosepalum*, eaten when the grass is dry, *Dichrostachys* leaves and pods, *Sclerocarya* and *Strychnos* fruit in the dry season. Estes noted *Diplorhynchus* being eaten in almost every sable area and also the common weed *Commelina*. Grobler (1974) noted the leaves of *Tarconanthus camphoratus*, *Dombeya* and *Grewia*.

The sable's need for water is another factor determining its distribution. Although it can walk considerable distances and, by resting in shade for the heat of the day, need only drink every other day, it will never be more than a day's journey from water. It sometimes drinks at night and Roberts (1951) described a herd approaching water with great caution, inching through the grass without a sound, "moving so slowly and silently as they emerged from the bush that they seemed not to be moving at all, except as time passed more and more of them appeared and those in front could be seen further from the bush".

The mobility of sable populations varies enormously. Herds in the Shimba Hills are thought to circulate over an area of some 13 sq. km but in other areas there are widely separate wet and dry season ranges (Estes and Estes, 1974). Grobler (1974) described breeding groups in Rhodesia that confined themselves to definite home ranges of 240–280 ha outside the dry season. Herd compositions vary from day to day as well as seasonally and Grobler recorded groups averaging six to fourteen animals during the height of the rains while calving was in progress. In March the mothers and Grobler recorded groups averaging six to 14 animals during the their home range. After the first fires in July the sable are attracted over greater distances on to grass flushes, where they form aggregations that occasionally number a hundred or more animals. At this time there may be a number of bulls accompanying the herds and these may be quite tolerant of one another although Verheyen (1951) noted them keeping well apart. Since the dry season aggregations may form on low-lying neutral areas in the vicinity of water this may influence the bulls' behaviour. Territorial intolerance might be linked with the incidence of females in



oestrous. Estes described "satellite" bulls showing submission to the dominant bulls within whose area they live. He suggested that since young males show a tendency to remain in the area they grew up in, the neophyte bulls may have been conditioned to submit to a particular resident bull, although in time such bulls become more established. Territories are known to have been held continuously for at least two years and are probably maintained by some individuals for very much longer.

In some areas sables walk up to 40 km when the rains begin (Verheyen, 1951), the herds returning then to higher ground. Here they often gaze over stony hillsides, steep valleys and plateaux, sometimes proceeding along regularly-used pathways between favourite grazing spots where herds or their subgroups may remain for several weeks on end. Their wet season circuits tend to be restricted by an active avoidance of rivers



and waterlogged drainage lines. Herds prefer the crest of wooded hillsides, dense shade and areas with an abundance of fallen *Brachystegia* to rest during the heat of the day. Estes and Estes (1974) noted that lone bulls in particular withdraw into thick cover to rest. These authors, Johnstone (1971) and Grobler (1974) charted the activity of sable herds and showed similar patterns of early morning and evening feeding. At times, notably during the full moon, the animals may be on the move at night but nocturnal activity has not been studied. Territorial males, however, are known to continue patrolling their territories at night.

Occasionally sable are aggressive towards other species and have been seen to threaten a warthog, kudu, zebra and even giraffe; these incidents tend to occur near water. Normally on their own, sable sometimes mix with other species during their dry season aggregations, notably with gnu, kongoni, zebra, eland and ostrich.

In the Shimba Hills Estes and Estes (1974) found that a single recognizable nursery herd ranged over approximately four male territories and they were able to map the home ranges of five nursery herds, finding little or no overlapping and no appreciable mixing of herds in this locality. Likewise, Grobler (1974) mapped the major home ranges of four breeding groups in the Matopos Park. Except for dry-season congregations on burns these breeding groups also remained distinct with very little overlap in range. Herds are generally between 5 and 10 km apart.



When a breeding herd first enters a territory the bull hastens to it and circulates among the females. His approach elicits urination and after putting his nose into the stream of urine the bull throws his head up in a dramatic *flehmen* gesture. Slowly the cows are circulated but only an oestrous female holds his attention and in herds with a well-defined breeding season his interest in the cows may be minimal outside the rut. Any tendency for the herd to drift too close to the boundaries of the territory tends to be checked by the male interposing himself between the herd and his boundary and turning the animals back with aggressive snorts and horn threats. So preoccupied does the bull become with retaining the herd within his territory that the activity often takes precedence over flight from danger and bulls are very much more approachable when tending a herd than when on their own.

I was once afforded a particularly vivid illustration of herding behaviour while watching a group of 34 sable in the Shimba Hills. These animals are well-habituated to cars and tourists and they were not unduly disturbed when a white car drew up; however, they fled down hill pell-mell when the car expelled a bright pink woman in a bathing costume who with mincing steps advanced on them with a cine-camera. As the herd drew near to the narrow forest defining the valley bottom, the male outflanked the herd at a furious gallop and halted the rout by vigorously threatening and chasing all the leading animals. The river course apparently marked

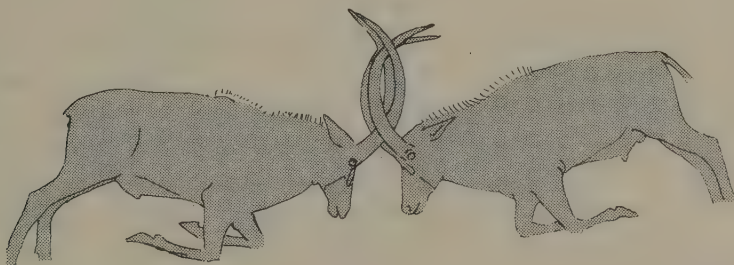


the boundary between this bull's territory and that of his neighbour on the next bluff: he energetically chased and threatened the reluctant herd for some 15 minutes until he had driven them back to the plateau in the centre of his territory. Once there, the bull ignored the herd completely as he grazed some hundred metres from them but still kept himself between them and his lower boundary.

The behaviour of the male while herding is modified by the age of the truant; he is most threatening against young males and adult females, rushing with his head held very low and the points of his horns directed at them, making loud bellowing grunts as he does so. They generally evade his attack by racing back into the tightly-bunched herd. The male tends to check his headlong rush before reaching any wandering juvenile and if it is very young the calf may appear to be quite unafraid of the bull. I once saw a bull nudge one very small animal with the curve of his horn, turning it back towards the bunched herd.

Females employ less conspicuous gestures than the males but dominance is betrayed by tilts and jabs of the horns and the carriage of the head. In fact, a proud horse-like stance and arching of the maned neck is the principal manifestation of dominance in both sexes in spite of its being rarer within the well-established female hierarchies. In fact, a territorial male keeps his neck upright and horns prominently to the fore even when cantering away from human intruders, a gait that earned the sable special admiration from the early horse-oriented explorers.

Males intimidate rivals as well as oestrous females with a lateral presentation in the proud posture. Fighting follows slow circling by both bulls accompanied by much pawing and tail lashing. A clash is preceded by shaking of heads and dropping on to the knees. The exact spacing of opponents is important and circling males may be so close that they have to back off before they can engage their long horns, and one function of kneeling may be to help fix the position and distance of competitors. Horns are of relatively even thickness and may absorb blows anywhere along their length. The horns are so strongly recurved that extreme retraction of the chin and head to the side or to the chest is a prerequisite for a slash with the sharp points. Engagement consists of a see-sawing linkage of the two horn arcs (see illustration).



When fighting is intense, such slashes are sometimes attempted but it is probably safer as well as more economic of energy to flex the neck less and exchange blows along the front curve of the horns. Hostilities are frequently interrupted by both competitors rising and resuming display; and



well-established neighbours rarely fight. Fatalities are known but appear to be rare. Fighting is accompanied by bellows and territorial males are also reported to be vocal at night, advertising their presence with snorts and grunts, particularly during the rut (Grobler, 1974).

Grobler reviewed breeding records from southern and central Africa to suggest that the rut reaches a well-defined peak at about the end of the rains, April—June. However Ansell (1960b) collected a wide scatter of breeding records from southern Africa which suggest that breeding patterns vary from year to year and from place to place. Lundholm (1949) also noted local variation but correlated breeding with regional climates and feeding cycles. The relationship between density and synchronized breeding that was recorded by Sekulic (1978), (see p. 549) may be very general in this species.

Sable antelopes do not possess facial glands but males have a pungent body smell. The male's attention to an oestrous female clearly frightens her at first. I have watched head-to-tail circling repeatedly terminate in the



female's lying down on the ground. The male's response to this tactic was to rouse her with pawing gestures, which then continued when the female was standing. I suggested earlier that *laufschlag* might derive from such pawing of the intimidated female and that its function in making the female lower her head and stand firm is particularly important in species where the females are horned, like the sable.

An oestrous cow often attempts to find refuge within the herd and the courting pair are seldom very far from the other females. Some older females may show an interest in the pursued female's urine but they do not curl the lip. Copulation is achieved in one swift movement and lasts no more than a few seconds.

There is an equal sex ratio and the young are 13–18 kg at birth. The mother generally leaves the group in order to give birth in thickets or other dense vegetation, where the calf remains hidden for about two weeks. The young calf makes a bird-like contact call and Grobler has described a short low grunt made by the mother searching for her young.

Estes and Estes (1974) noted that the mothers formed small subgroups and their young, which may be hidden close to one another, also associate at an early age. For example, he saw two very small calves lying and moving about together by moonlight after their mothers had suckled and left them. When alarmed, the young get into grass and crouch relying on immobility and their sandy colouring to pass unnoticed. If captured, they make a loud distress call and Verheyen (1951) described adults driving off two leopards that had grabbed a young sable; the calf was apparently unconscious from the shock of the attack but it revived and joined the herd. On the other hand, Grobler (1974) in the course of tagging many calves noted only two adult females that showed any sign of defending a calf. Age-grouping is conspicuous once the mothers and young have rejoined the main herd anything up to two months after the births and the calves may trail in the rear, which Estes attributes to their sleeping more and feeding less than the adults. All ages, but particularly the younger animals, make a curious high-pitched note which alerts the entire herd. This might derive from an infantile call.

In the Kruger Park, where lions are more numerous than in many parts of the sable's range, there are localities where more than eight times as many sable are killed than their abundance would merit on a strictly proportional basis and the sable are by no means common, representing only 0.58% of the lions' possible prey species (Pienaar, 1969a). Since large carnivores live at low densities in most parts of the *miombo* woodlands it is possible that the sable is adapted to a low level of predation.

Grobler and Wilson (1972) found that sable were a significant part of the leopard's diet in the Matopos Park and Johnstone (1971) noted hyaena predation, although this animal is scarce in *miombo* country.

The population dynamics of the species has not been studied in any detail but Grobler (1974) showed that an equal sex ratio was maintained in the yearling age class in the Matopos Park but that the percentage of calves dropped from 26–29% in the first year down to 10–19% a year later. Of the remaining adults a female ratio of 36–49% as against 3–11% males betrays a remarkable decrease in the male population. Estes and Estes (1970) found a similar adult-female ratio when they listed overall population structures for counts made in southern Africa but adult males accounted for 3–30%, a variability that might very well reflect the males' varying fortunes in different habitats and localities.

Blackmore (1962) described and photographed an adult male sable rushing a lioness but the dispersed and solitary males are clearly more vulnerable than members of the herd.

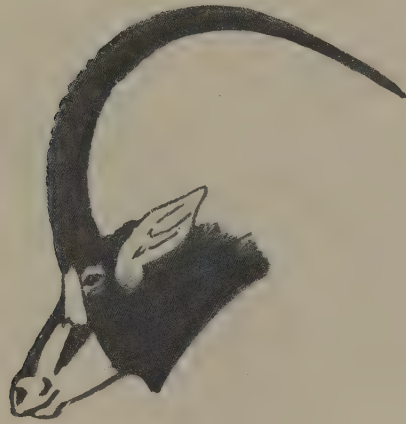
The animal figured in this profile was a territorial male known to have occupied a very small area of a few hectares for at least six months. Two vehicles passing through his area one evening led to his fleeing for a considerable distance. That night he was severely mauled by lions and it is possible that his vulnerability was increased once he was out of his known home range. Notwithstanding his wounds, he was back in the centre of his territory two days later.

Territorial bulls are also vulnerable because they are a favourite trophy for motorized hunters. A guide in the Chuya area told me that a local

missionary doctor succeeded in wounding (and losing) three sable bulls in one day's shooting from a Land-Rover; and in some areas it is possible that this sort of drain on territorial sable populations might be on a significant scale.

Of great import for the species is the tendency for new settlements to monopolize watering points, to cultivate the best pockets of soil and to remove tree cover, activities that strike at the sable's dry-season dependence on water, its wet-season grazing and its overall ecological needs.

At present, tse-tse throughout the *miombo* belts puts limits on settlement and the species is therefore still widely distributed in Tanzania.





**Horse
Antelope,
Roan Antelope
(*Hippotragus
equinus*)**

Family

Bovidae

Order

Artiodactyla

Local names

Korongo (Kiswahili and many other languages), Abu-uruf (Arabic), Bwore (Lwo), Echilil (Ateso), Echolia (Karamojong), Oforo (Lugbara).

Horse Antelope, Roan Antelope (*Hippotragus equinus*)

Measurements head and body

190—240 cm

height

126—145 cm

tail

37—48 cm

weight

280 (242—300) kg males

260 (223—280) kg females

horns

55—99 cm

Races

Hippotragus equinus langheldi

East Africa

Hippotragus equinus bakeri

Northern Uganda

Literal translation of the scientific name of the roan is the “horse-like horned horse”. This name stresses a resemblance that is more than superficial, for of all the hippotragines this species has converged most with horses and fills a similar grazing niche. It is possible that this parallelism may be relevant to several aspects of the roan’s general biology including its distribution.

Both sexes are very similar but the male is more heavily built, particularly in the horns, head and neck. The male’s black and white facial markings also tend to show more contrast and in this species the signalling system is almost entirely concentrated in movements of the head, ears and tail. The body is sandy-fawn, a good camouflage when the animal is still.

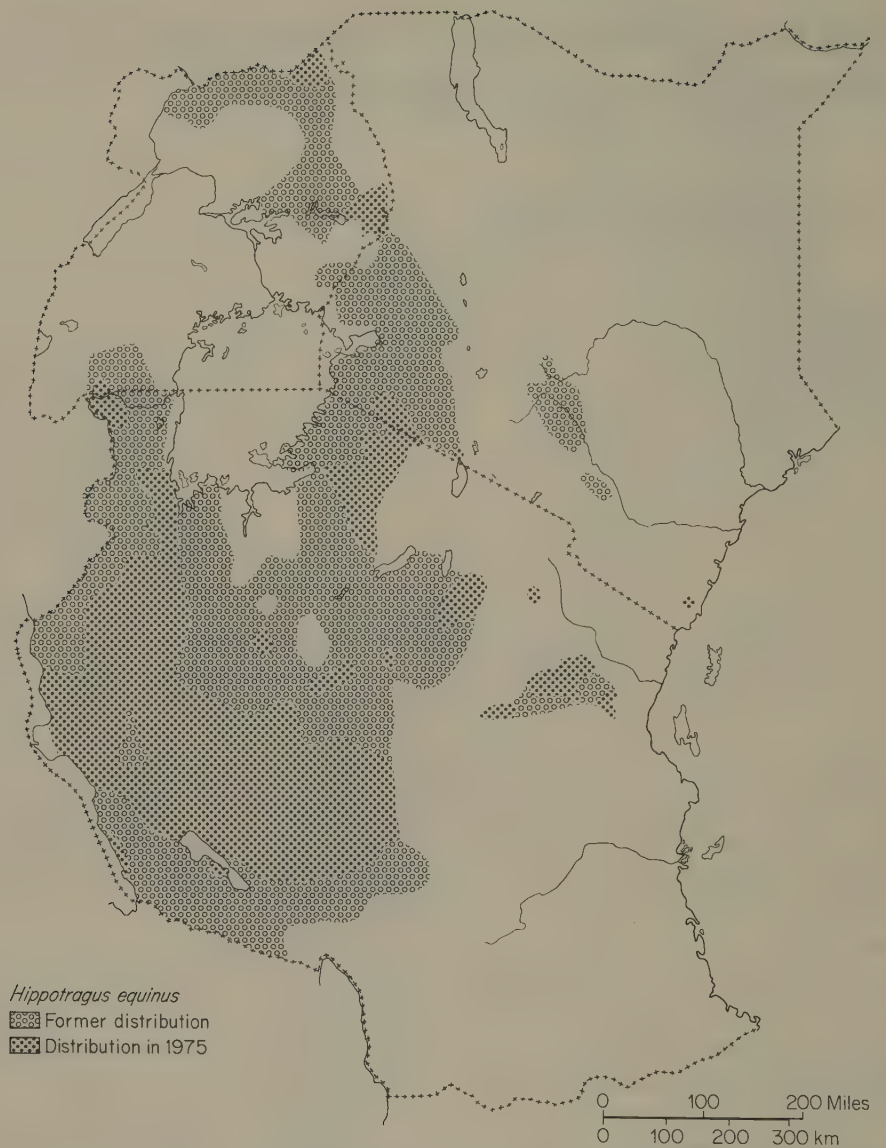
Roan antelopes originally occurred over a very wide range of moist wooded grasslands and they were once common all over the better watered areas of the northern savannas, between the tropical forests and the Sahara. In the southern savannas its distribution seems to have been more patchy and it has apparently been absent from large areas on the eastern side of the continent for as long as there have been records.

In East Africa there are few places where they are very numerous but local residents frequently assert that where roan are present, herds have always lived in the same localities and that such fluctuations in numbers that have occurred have never led to the formation or amalgamation of exceptionally big herds.

It is not surprising that a pigmy antelope should be attached to its little territory, yet it is conceivable that the advantages of knowing a home range intimately can be equally important to groups of larger animals, particularly if the species is less active than its competitors and more vulnerable to predators or disease. The disappearance of many roan antelopes from a herd



Total range of
Hippotragus equinus
in the twentieth century



that had been artificially transplanted in Kenya could suggest that an already low survival rate was lowered still further by removal from their traditional grazing grounds.

It has been argued by Joubert (1974) that it is intolerance of the males towards one another and the existence of what may be closed social units among the hierarchically organized females that is responsible for the sparse distribution of herds in southern and eastern Africa and that an exclusive use of relatively large areas of favoured habitat by a single herd puts a restriction on population size. He also points to a high reproductive potential in this species, with each female producing young at least once a year. Yet the population buildups seen in so many other species have not been recorded for roan antelopes. Joubert suggested that numbers might be regulated by a combination of ecological limitations affecting the carrying capacity of their habitat and a social system that spaces the population at a comparatively low density.

There has been no published work on the population dynamics of the roan and the detailed role of disease, predation and competition from other species awaits investigation. In any case these factors would vary greatly from place to place and the roan would need to be studied in the context of different ungulate communities for a really satisfactory picture of its biology. Roan are known to have been a dominant species in certain restricted localities, for example 6,000 to 8,000 were recorded in the Waza National Park in Cameroun and although this park covers 1,700 sq. km, the actual density of these antelopes would have been high, for a large area must have been denied to them during extensive seasonal flooding (to which the two other dominant species, kob and topi are better adapted).

It may be significant for the roan's dominance at Waza that the zebra is absent, for this animal may be the roan's most important competitor. The sable, sometimes discussed in these terms, (Lundholm, 1949) is more an animal of the woodlands, shunning open grasslands, so that direct competition is generally avoided. Herds of zebra, on the other hand, probably monopolize large areas of grazing that might otherwise be available to the roan. Where the two species occur together some ecological separation can be detected. Irrespective of intraspecific social factors the overall density of the roan will be dependent on the feeding resources of the home range at the worst time of the year, while the mobile zebras, bulk grazers and free to find the best seasonal grazing, can sustain much higher numbers. Furthermore, they are faster and more alert and so might be proportionately less vulnerable. Zebras also bunch to escape predators, while roan often scatter in alarm, which makes the young easier to isolate and attack. I have seen a pack of wild dogs harassing a herd of roan out on an open moonlit *mbuga*. The outcome was not seen but there could be little doubt about the seriousness of the threat that the dogs presented.

Roan are most characteristic of thinly tree'd grasslands, park-like savannas that are often dominated by *Commiphora* or, to the south, *Colophospermum*. In the extensive areas of East African uplands they used to be conspicuously successful members of a community that included buffalo, mountain reedbuck, eland and hartebeest as well as zebra. Here the grassland has forest relics or an irregular scattering of fire-resistant trees such as *Dombeya* and *Uapaca*. Tree clumps and the forest edges are favourite foci for the roan and they seem to need trees and scrub for shady cover or undisturbed rest.

They have been recorded grazing on *Themeda*, *Hyparrhenia*, *Panicum*, *Heteropogon*, *Digitaria*, *Eragrostis* and *Cenchrus*. Medium to short lengths are favoured. In addition to grass they take various herbs and occasionally browse shrubs and trees, notably *Colophospermum*, *Grewia*, *Thylacium*, *Lonchocarpus* and *Kigelia*. They are also fond of picking up *Acacia* pods in the dry season and they have been seen feeding on mushrooms.

Joubert (1974) suggested that the roan is a selective feeder but, since its favoured grasses are often dominants in their relatively rich rangelands, it cannot be described as a specialist and its limitations are unlikely to be founded on diet.

Joubert (1974) found that in the course of daily feeding a herd moved 2—4 km from its watering point. The amount of ground covered varies



with the season, the state of the grass and with the amount of disturbance they suffer from man, predators and perhaps other ungulates. An area of cushion grass near the waterhole may hold them for several days, and Child and Wilson (1964a) watched a herd of roan feeding on the aquatic plant *Equisetum*: the animals submerged their heads for as long as 48 seconds while gathering mouthfuls under water.

They drink regularly and in great quantity, sometimes visiting water twice a day. Nonetheless, they can go without water every other day during the dry season. They visit mineral licks and are said to chew at old bones. A lactating female has been noted eating soil with some avidity (Henshaw and Ayeni, 1971). Drying of waterholes or severe scarcity of grazing occasionally brings roan together into aggregations of up to 150 individuals. At such times all the assembled animals can be described as being dependent on the same local resources but it is uncertain to what extent they are representative of a discrete regional population. Verheyen (1951) described seeing a large herd fragment into smaller groups at night only to converge again in the morning. During the day he saw several adult males keeping well apart but within sight of the herd, yet each was associated with one of the smaller groups during the night.

The size of herds at any one time of the year might be influenced by the distribution of water and grazing and also by seasonal changes in the reproductive cycle, which might intensify male competition for females but the most commonly seen numbers are 4–18 females with young accompanied by a single adult male. Backhaus (1959) suggested that both the female nursery groups and the bachelors establish hierarchies, probably on an age basis. Joubert (1974) described low intensity fighting as being most frequent among immature animals and constant skirmishing between the bachelors, which results in a social ranking order among all the members of a group. He found that the females of a herd kept in an enclosure maintained a consistent hierarchy over several years and he suggested that roan herds are stable and exclusive social units. However, he observed a reversal in the roles of two adult males in the enclosure. Over a period of 2 or 3 months the herd bull was ousted by a lone male that had previously hung about on the peripheries of the herd. Both the enclosed animals and unrestricted bulls in the Kruger Park were seen to defend the area around a herd of females but no bull defended a fixed area for which boundaries could be drawn, a respect in which roan are quite different from sable antelopes.

The attachment of a herd of roan antelopes to a particular locality is not reinforced by intense herding behaviour on the part of a bull, indeed, apart from his intolerance of other males, the herd bull's behaviour is not dissimilar to that of a top ranking female. Occasionally he may even initiate movements and be followed, in spite of this being the normal prerogative of the leading cow.

Individual Kruger Park herds have been estimated to range over total areas averaging 80 (range 66–104) sq. km in the course of a year with minimal overlap in their zones of activity (Joubert, 1974) but throughout Africa herds are commonly seen to restrict their activity to the immediate vicinity of a drinking point with sudden moves to relatively distant localities.

Sometimes the moves may coincide with a change in the seasons but at other times there is no obvious explanation for the decamp.

Solitary males and bachelor groups are not infrequently observed near herds. Although the outsiders share the species' general attachment to traditional roan localities they are not tied to an area as territorial species are and, like the female herds, they are known to wander, although the extent of their movements has not been measured. Jackson (1930) working in a good roan locality, could recognize some individuals which had very regular habits and would be seen continually passing or standing about along established routes that lay between their wooded resting areas and the open *mbuga* where they grazed in the dry season. Jackson thought that other animals were not resident but visitors or intruders passing through the area. Joubert (1974) recorded overlaps in the zones of activity of different herds but he described intruders as always being at a disadvantage if the herds met.

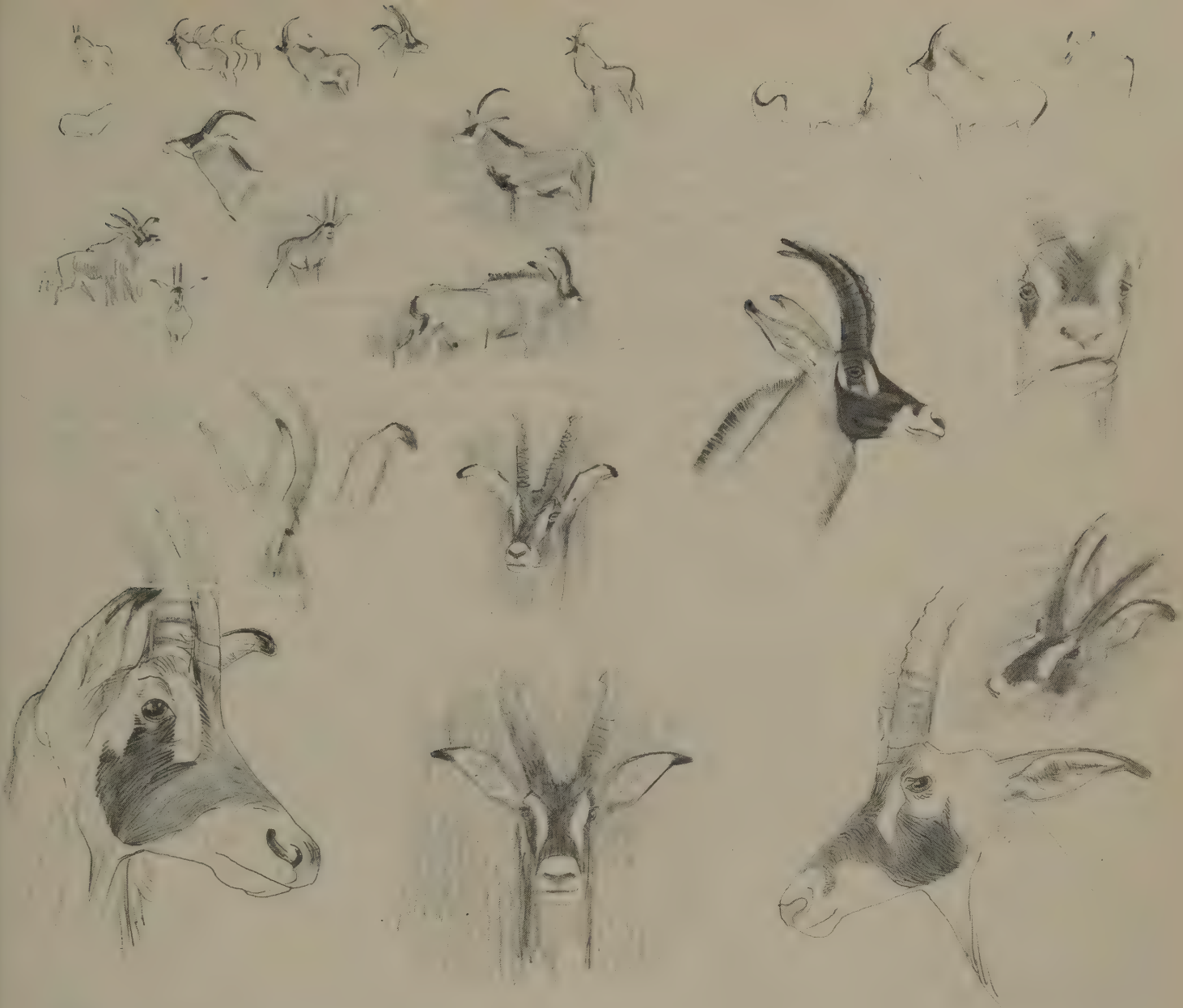
Frequent changes are likely amongst the males accompanying female groups. Also the bigger herds can be predicted to splinter when they become larger than a single male can effectively defend and this may be the main determinant of numbers in a herd.

Solitary bulls can be aggressive and not only to their own species. An old male enclosed on a stock farm in Uganda chased workers up trees and on one occasion pursued a man up to his hut, after which the bull charged the hut wall repeatedly.

Like most antelopes roan grate and thrash their corrugated horns against trees and bushes and mature males horn the ground as well, a practice which greatly reduces the length and blunts the tips of the old males' horns as well as grinding down the annulated surfaces.

Intraspecific contests can be severe and Roberts (1951) described seeing a patch of ground extensively ploughed up and bloodied during a fight. Verheyen (1951) saw a fight give way to side by side pushing contests in a standing position in which weight was decisive. He saw contestants break off fights and exhibit a lateral presentation, tilting the head so that the horns were pointed at the adversary.

The massive reinforcement of their horn bosses reflects a different fighting technique from that of the sable. Approaching with lowered head, they suddenly bound forward dropping on their knees as they clash their foreheads and horns violently together. Several observers have described them looking stunned after the impact, but the whole performance is repeated and when horns are engaged, sudden violent thrusts may make the opponent stumble or move back. Such hostilities between antagonistic bulls are sometimes preceded or replaced by strutting in the lateral presentation, and the facial markings appear to act as target areas in encounters between the younger males, which rub and push at one another's faces before the fight and during intervals. Their ears move continuously and the vertical erect ears signify submission, while more horizontal ears with a backward sweep to their curved, pointed tips implies dominance. As with so many animals, submission is betrayed by the tail held tightly between the legs while a confident animal holds its dark-tufted tail out or lashes it about.



In the routine interactions between members of a herd, the inferior animal approaches or passes with lowered head.

The courtship of the roan has been described by Verheyen (1951). The male circles the standing female with slow hesitant steps while she follows his progress with her eyes; if he can get into a position to do so, he starts striking out at the female's hindleg with his foreleg, a gentle form of *laufschi-lag*. If circling is continued, each partner may smell the other's genitalia and the male may rest his head on the female's back. When the female is ready, she lowers her neck, takes a broader stance and twists her raised tail to the side. He mounts her rapidly with the head raised and body bunched.

Breeding takes place throughout the year but births are rare in the dry season. In the more southerly latitudes most births occur between September and April. Verheyen (1951) reported that pairing was most noticeable between May and August. Females are capable of reproduction at the age of two years and tend to come into oestrus again two weeks to four months

after giving birth. The gestation period is about 275 days. Parturition takes place in seclusion amidst tall grass or thicket and after a short spell of isolation both animals rejoin other females and their young in a herd.

At birth the young has the head and body length of 33 cm. It suckles resting on the carpal joints. After a few weeks it starts to chew greenery, spending much time in mastication. Once the horns appear, the calves within a nursery herd form age groups. Sexual segregation is already apparent, the young males spending much time down on their knees sparring with foreheads and horn buds.

The young are probably vulnerable to a wide range of predators. Like the adults they are surefooted and reasonably long-winded but the maximum speed of adults is about 57 km per hour, which is slower than zebras and many other ungulates that are commonly preyed on by lions, hyaenas and wild dogs.

Pienaar (1969a 1974) pointed out the tendency for a herd to scatter in fright and his records of predation in the Kruger Park suggest that lions are the main predators in that region with occasional kills by leopards, cheetah and wild dogs.

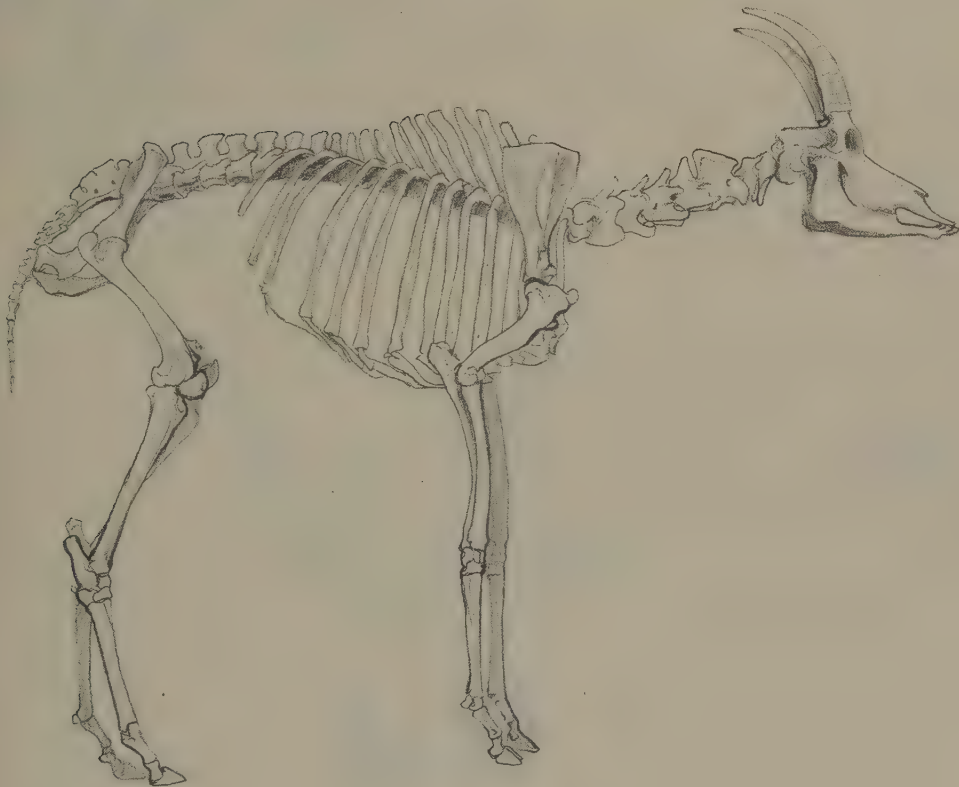
Guggisberg (1963) reports a pair of lions attempting to stalk a herd of roan. After some signs of nervousness the herd suddenly wheeled round and advanced on a broad front forcing the lions to retreat and then again turned to face them after a second advance; hunters too are not infrequently charged by wounded males. An illustration of this animal resorting to a more primitive means of defence occurred during a tribal hunt in Madi, when a roan was entangled in a net. The hunter who tried to spear this animal was so badly bitten on the arse that he spent a month in hospital.



So long as the miombo woodlands remain relatively underdeveloped because of tse-tse fly, the roan antelope will probably continue to inhabit the *Combretum* and *Acacia* fringes to the drainage lines. Elsewhere they have already seen a widespread decline. One cause of the roan's retreat is its preference for fertile, well watered land that is not subject to waterlogging in the wet season, nor to desiccation in the dry. Such conditions especially favour "roan country" for pioneer agriculture. An apt illustration of this was provided by my son's unearthing an old roan skull on our farm, where the land has been cultivated for 60 years.

Expensive "rescue operations" have been mounted in the past to move entire herds from settlement areas. In the absence of fundamental biological data on the species one cannot but remark that the funds would have been better spent on a detailed study of the roan.

The species does well when effectively protected in suitable sanctuaries and it appears to flourish in captivity but is dangerous to handle.





Oryx

(*Oryx gazella*)

Local names

Choroa, Barabara (Kiswahili), Biid (Somali), Edirr (Turkana and Karamojong), Olgemas orok (Masai), Gialauk (Kidorobo), Sala (Kiliangulu).

Measurements

head and body

153—170 cm

height

120 cm

tail

47 cm

weight

176 (167—209) kg males

162 (116—188) kg males

horns

65—110 cm

Races

Oryx gazella beisa Eastern Uganda and northern Kenya

Oryx gazella callotis Southern Kenya and north-eastern Tanzania

The oryx is one of the few true desert-adapted mammals to occur in East Africa, where it generally lives in rather less demanding habitats than its relatives do in the Sahara and Arabia. The animal is muscular and compact. The tall spines of the thoracic vertebrae form a hump over the shoulders and the nuchal ligament connecting this with the back of the head and neck vertebrae gives exceptional depth to the neck, making it rather horse-like. The oryx has a large heart and lungs, which are contained within a barrel-like body; as a consequence its legs are widely spaced. The length of the legs is evidently a compromise, having been reduced so that the weight of the big hoof does not slow down the recovery phase nor waste energy, yet they retain a long stride. The result of these anatomical modifications is a peculiar but fast gait with great stability (useful on rough stony ground) and a striking body build.

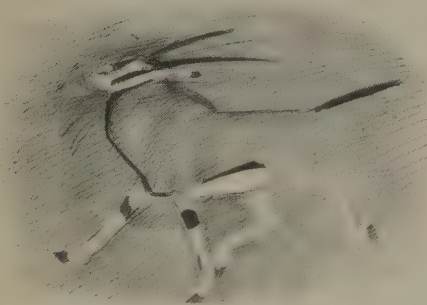
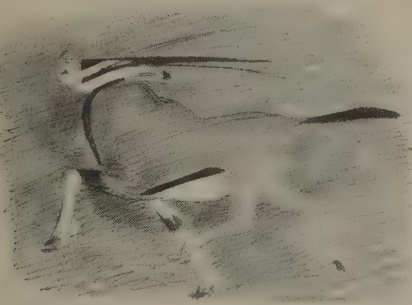
The oryx has a clearly demarcated black and white head in which the long line of the horns is continued right across the face in the form of a black stripe. There is another strong contrast in the pied foreleg. In profile the depth of the shoulder and neck are emphasized by a mane and strategically placed black lines, one down the throat, the others across each flank, slanting down from the top of the thigh to the breast and separating the fawn body colour from the white belly. Apart from the black tail, the hindquarters are neutral. Visual emphasis of the horns and of the shoulder

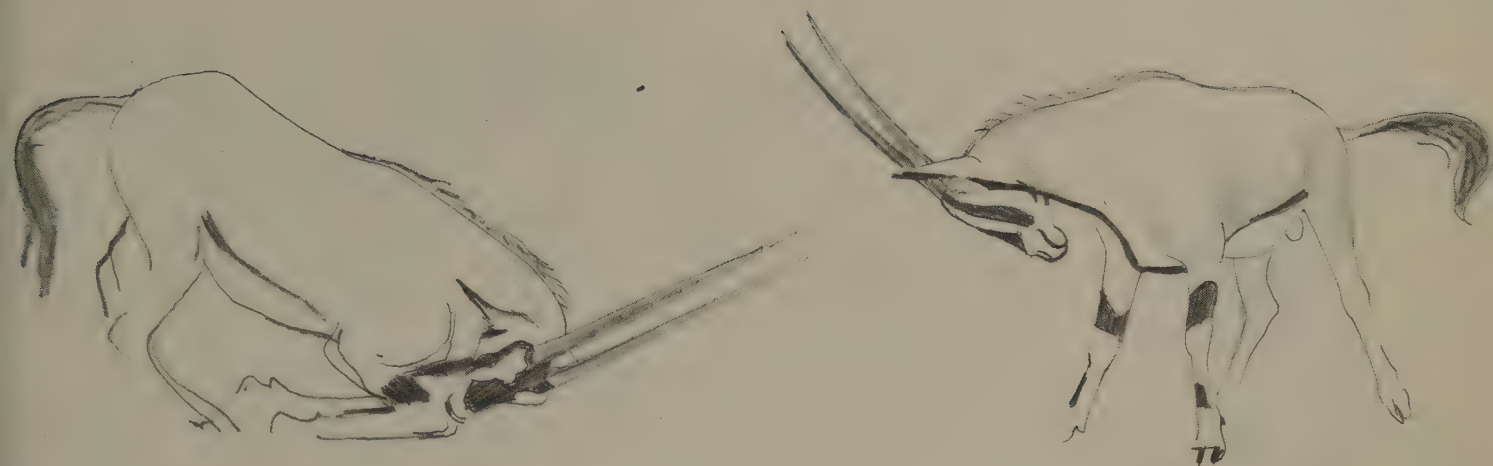
mass is common in the bulls of many bovid species where it undoubtedly reinforces male dominance. In the oryx both sexes are identically marked and males are difficult to tell from females unless they are fully mature and sexually active, in which case their thicker horns and necks, prominent genitalia or ostentatious behaviour distinguishes them. Females have horns as long as or even longer than males but rather more slender.

The lack of sexual dimorphism can probably be correlated with the existence of a female hierarchy and intergroup intolerance. The implications of exclusive groups and hierarchical organization may also have an indirect reference for the striking colour scheme of the oryx. The markings of the face, forelegs and tail stand out from an otherwise neutral coloured body and the bold linear pointers on the neck and flanks ensure that postures can be interpreted easily, even from a distance. For example, submissive animals lower the head or may squat as if to excrete: both gestures alter radically the linear semaphore of neck and flank stripes. By contrast, aggressive animals hold their heads up, bunch the neck and walk with slow, high steps. Short sharp movements of the head flaunt the length of the horns while they also flag the markings of the face. Rivals walk around one another tense and slow, occasionally one may paw or even horn the ground. If they finally clash, males often use their horns like staves to strike or fend off blows. If horns are engaged when the heads are lowered they may be swept sideways or twisted rather than stabbed. The effort seems to be directed more towards throwing the rival off balance rather than skewering him. An aggressive male will smack its horns down against an opponent, which must quickly parry the blow or be struck on the neck or sides.

Bovoid bulls commonly adopt a ritualized gait and circle rivals or females, thus allowing a broadside view of their intimidating characteristics to take effect. A confrontation or submission may be elicited from the object of this lateral display. If a cow or inferior male then prostrates itself the dominant animal may then attempt to rouse it with pawing gestures. Yet all classes (particularly young ones) advertise themselves with a ritualized lateral display and the pattern elements serve to exaggerate the length of the horns, the bulk of the forequarters and, when the knees are raised, the power of the forelegs. While the numerous stotting, pronking, leaping, cavorting and prancing gaits of gazelles, reedbuck, hartebeest, gnu, sable etc. are all self-advertising they seem to originate from the exaggeration of specifically different actions to serve quite diverse types of social behaviour and organization. Small but frequent gestures of the head and horns suggest that latent threats punctuate the day to day activities of most members of the herd but rank contests are most explicit in the frequency of clashes amongst the young and in "tournaments" which are peculiar to the oryx and are generally set off by an abrupt change in the environment, such as a sudden wind, a shower of rain or a release of tension or excitement in one or more youngsters.

A tournament starts with one or more animals running round the herd in broad circles. A galloping spurt seems to build up a performer's momentum before it suddenly changes into a long high-stepping pace like a hackney pony. Simultaneously the animal hunches its neck back and throwing its chin up in the air swings its head from side to side in rhythm



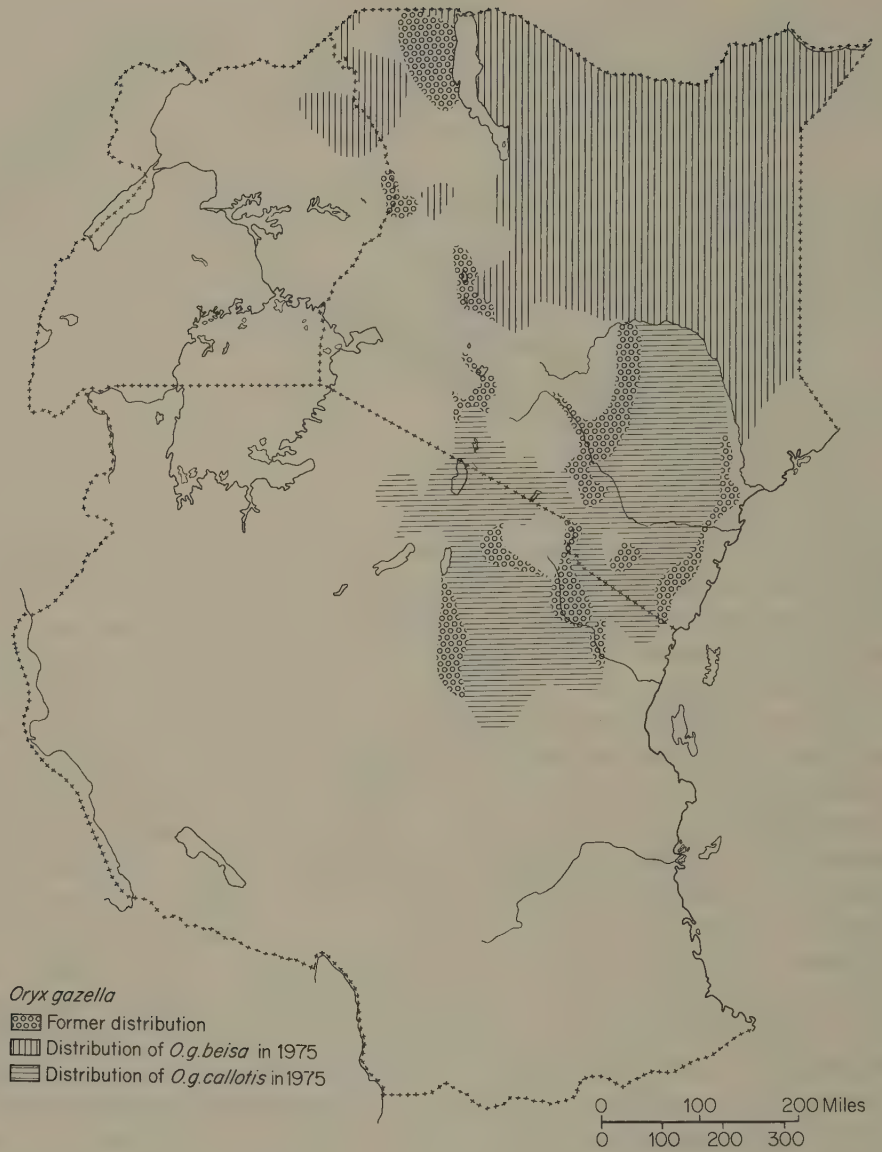


with the pace of the forelegs, so that the black and white of the head flashes in time with the knees and forward flying hooves.

The fact that the stripes on the face continue the horizontal line of the horns might improve the coherence of the signal through following the plane of movement.

The circling is interrupted by feints towards individuals in the herd and the hackney pace may terminate abruptly in a clash. In this display, which Lewis (1974) terms "runplay", even juveniles appear to provoke clashes without regard for the status of their seniors and the impression is of a distinctly playful activity. Excitement may spread until many members of the herd are running around in circles with sudden spurts of galloping and ritualized pacing interspersed with brief horn clashes between different runners or against static members of the herd. In both action and sequence the display resembles a vastly speeded up version of a male challenge with the final clash generally the most abbreviated element of all. Animals that are challenged may simply fend off the collision with their horns, may actively avoid it or they may respond. The tournament seems to function as a highly ritualized device for testing rank order. It is the ritual that minimizes the risks of conflict between such dangerously horned animals and allows a wide range of ages and sexes to participate. Young animals literally go through their paces and have the opportunity to exercise their physique as well as their aggression while establishing their place in the herd. The speed at which the tournament is conducted also contracts the amount of time and energy spent on settling hierarchy. For a desert dweller with dispersed food and excessive heat to contend with this might be an important consideration, for long periods of feeding and resting are necessary. The fact that Lewis (1975) saw tournament behaviour in the early morning or at the start of a rain storm is consistent with this idea.

The dominance displays of all the hippotragine species involve an emphasis of the forequarters but the placing and alignment of the oryx's piebald flashes and lines have probably evolved in close connexion with the behaviour of the tournament, most particularly with the ritualized movements of the legs and face.



The gazelline oryx has three distinct populations: the gemsbok, *O. g. gazella*, of the Kalahari which is sometimes treated as a distinct species, *O. g. beisa* of the Horn of Africa and the fringe-eared, *O. g. callotis*, south of the Tana River.

The distribution betrays the existence of drier climates in the past, some of the implications of which were discussed in Vol. I (pp. 62—63). East African oryx live in a variety of habitats, from the stony deserts of northern Kenya to the much less exacting acacia scrub and dry thickets of further south. Nonetheless, their presence in an area is a clear indication of heat, for oryx probably lose their advantage over competitors if an area is not seasonally arid.

Like sable and roan antelopes they are not discriminating grazers and crop a wide range of grass species and growth stages, taking a succession of small bites. Recorded grasses include *Aristida*, *Sporobolus*, *Setaria* and

Chrysopogon but the actual number of species is probably very great. Browsing off *Acacia*, *Adenia globosa* and *Disperma* has also been recorded. Root (1972) described them during a severe drought digging to a depth of 20 cm with their hooves for the tubers and swollen underground stems of *Thunbergia guerkeana* and *Pyrenacantha malvifolia*.

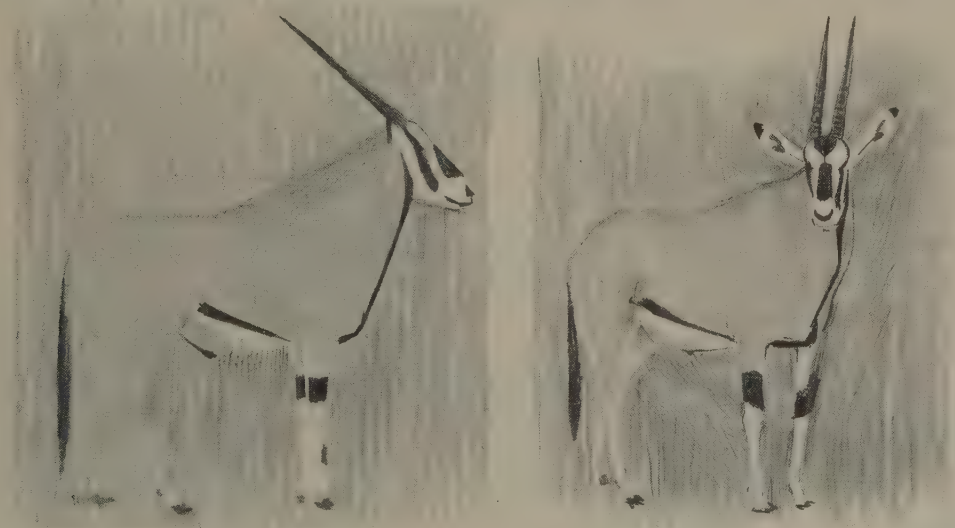
Cobb (1976) found that oryx in Tsavo took more browse in the dry season but avoided tall shrub cover just as they avoided taller grassland in the rains. This may be an avoidance of predators. Tsavo oryx prefer high-protein grasses such as *Brachiaria* and *Schoenfeldia* and the shrubs *Grewia* and *Indigofera*.

Where conditions are suitable oryx may remain in a locality over several seasons but their social behaviour probably accommodates readily to a nomadic existence and cyclic movements have been recorded in several areas.

Percival (1928) stressed the irregular wandering habits of the oryx in northern Kenya with large numbers being found in a district one year and none the next, at which time they are to be seen in another area. The Uganda population makes seasonal movements which are probably influenced both by the state of the ground and by grazing conditions. They avoid the low-lying flats throughout the rains and are found at this time on several separate areas of higher ground but visit the Matheniko flats and Turkana in the dry season. A similar pattern can be seen in northern Tanzania, where the oryx join other animals in northern Tarangire and in the Olgarwa Shambalai depression during the dry season. Unlike most of the other animals they are not attracted to these dry season concentration areas by water but rather by the improved grazing conditions created by the presence of many other grazers. The same areas are uninhabitable for the oryx in the wet season because of waterlogging.

The oryx's dislike for soft, wet ground may be related to the structure of the hoof, which is exceptionally large for its size and is probably best adapted for firm or stony ground.

Herds of females with young are sometimes seen without any male in attendance and dominant males have not been seen to attempt to coerce





nursery herds in the way sable do but herds of females and young often include many males that are long-horned and apparently adult-sized but are not in reproductive condition. It is not known whether these mixed herds are temporary associations between nursery and bachelor herds but the latter do occur.

Herds are commonly of mixed sex and number 20—60. Temporary aggregations of over 200 have been observed. Small domestic herds studied on a ranch by Stanley Price (1978) were dominated by a single alpha male. Usually there was a beta male as well. Thereafter there was a strictly linear female hierarchy based on age or length of residence. All other males ranked below any adult female. The herds tended to be stable over fairly long periods and were of closed membership. Strange adult females were repelled but submissive males were more easily accepted. Tolerance of juveniles is striking but declines fast after one year of age. Newly introduced animals shield themselves from aggression by associating with calves. The social behaviour of domestic oryx seems to be consistent with casual observations of structure in wild herds. As a class males are probably much less permanently attached to a social group than females and are the only animals to remain solitary for any period of time.

Oryx have an immediate post-partum oestrus and bulls generally attend a cow closely immediately after birth, probably inseminating her within a week or two of parturition. As the female remains in relative isolation from the herd during this period, the reproductive advantage of having female groups herded by a bull is somewhat diminished and the premium is upon a male identifying the newly delivered mother, in spite of her seeking out less exposed habitats to hide her new calf in. The attendance of the male might be thought to have a protective advantage for the young but in my own experience both adults tend to abandon the young if approached and the latter relies upon lying flat and still to escape detection.

The female may repel the male with repeated frontal clashes but the courtship tends to fall into an awkward circling as the male attempts to sniff and rub her perineal area. The male walks with head erect or out-stretched while the female keeps her head down in an attitude of submission throughout the period of courtship and captive females have been seen to lie down and bawl. Oryx follow the usual sequence of *laufs Schlag*, firm standing with well spaced legs and the male performs a rapid, very erect mounting.

Births occur throughout the year but have been recorded as being much more in evidence during the wet season in Karamoja. Gestation ranges from 265 to 300 days but estimates of 210 days have been published. Assuming a high proportion of successful conceptions during the post-partum oestrus, births become staggered over the years and crops of rainy season births in Uganda need explanation. Of this as well as other aspects of the oryx's biology much remains to be learnt.

Calves are more tawny in colour than the adults and they lie concealed for up to three weeks after birth, only rising to suck from the mother. The markings are scarcely visible at this stage but develop rapidly once the calf is a mobile member of the herd. A very high mortality is thought to occur during the lying-up period.

Cheetahs are known to run down young animals, and hyaenas, leopards and smaller predators are likely to take the calves. Lions kill a number of



adult oryx in localities where both species are common but large predators are generally scarcer in the habitats where oryx are found. Writers that have ascribed great stamina to the oryx have been contradicted by others asserting that it tires quickly. If a fast vehicle chases a wretched animal on a hot afternoon, when it would normally be resting quietly in the shade, it is not surprising that the animal eventually comes to a standstill.

Taylor (1968a) has studied water balance and temperature regulation in the oryx and discovered that when the oryx was deprived of water its temperature could rise over 45°C . without ill effect and that this heat dissipated at night by conduction and radiation. Once the body temperature is over 41°C the dehydrated oryx pants whereas the watered animal sweats. Taylor measured a saving in water loss of nearly 60% in a dehydrated animal



and he remarked that its skin gave the impression of being drier and less permeable.

When undisturbed oryx tend to move in single file and spread out when they start grazing. When disturbed they will generally flee but in certain circumstances they turn to the attack and lions have been seen to die of oryx wounds. Percival (1928) pointed out that even in the open country an adult oryx will emerge from the herd to fight a small dog, rushing at it and making circular sweeps of the horns. When conservation officials were attempting to round up *O. g. gazella* in the Namib desert their vehicles were attacked by the gemsbok. When wounded they have been heard to bawl but otherwise appear to be rather silent.

The oryx has been virtually exterminated by the tribesmen living west of Lake Turkana, they exploit the oryx's defensive behaviour with dogs. This behaviour probably evolved as an effective defence against hyaenas and wild dogs, *Lycaon*, but the Turkana dogs bring an animal to bay, which allows the spearmen to run up and dispatch it. The Turkana and Karamojong hunt oryx not only for the meat but for the hide of the males for their shields. This skin is exceptionally tough and is over 6 mm thick on the neck and sides. This feature is less developed in females and appears to be an adaptation to protect tissues from bruising by horn blows and from the occasional jab. Few dermal coverings could stop a determined thrust with the point of the horn but the species' ritualization of fighting probably helps to avoid this risk.

Oryx horns have had a phallic significance for many cultures and they are sought after as charms even in regions where the animal itself is unknown. In this way oryx horns found their way to mediaeval Europe where they were passed off as the spikes of unicorns. The symbolism may not be entirely absent today, for stuffed heads in Nairobi taxidermy shops betray that the oryx is still a favourite trophy.

In ancient Egypt, paintings and hieroglyphs show that great herds of oryx were kept in domestication. According to Joleaud (1918) mutton and oryx meat were in the regular diet of Solomon's household and the animal is one of the most ancient semi-domesticated animals. Roman mosaics show that *Oryx leucoryx* occurred in North Africa during imperial times and Juvenal discussed the approval given its meat by gourmets.

Considering the animal's ready acceptance of domestication and its physiological adaptations to living in the desert, it is ironic that it should be deliberately exterminated in the very regions where devastating famines are being experienced.

Since 1970 an attempt has been made to domesticate a small herd of oryx on the Galana ranch in Kenya. The animals are tended by a herdsman and corralled at night and Lewis (1975) is confident that this species can be usefully domesticated and run with cattle on very dry ranges. It is paradoxical that efforts at domestication have been pursued with enthusiasm and at no little cost before the animal's natural history and social behaviour in the wild have been studied. There has been no attempt to determine the ecological and behavioural limits of wild populations, which are migratory to a greater or lesser degree and live at variable densities across a wide range of habitats.

Since this was written studies of oryx have been initiated by M. Stanley-Price in Kenya and Oman.



Sheep and Goats, Caprines

Caprini

The Caprini are only represented in East Africa by domestic sheep and goats.

Miocene fossils have been described from several parts of the Ethiopian region, mostly from dry, more mountainous North Africa but the history of the tribe is almost wholly Eurasian (and latterly North American).

Gentry (1970a) described *Oioceros tanyceras*, a fossil from Fort Ternan (about 14 million years) as a caprine and he considered that this species could be ancestral to the Alcelaphini.

Differences between the contemporary representatives of these tribes are so great as to make this suggestion appear very far-fetched but consideration of the broadest ecological trends in bovid evolution suggest that Gentry, who based his idea on a close examination of Miocene fossils, was probably right about the common origins of the two groups, but I consider that their common ancestry will be found *before* the emergence of a recognizable caprine lineage and *after* the splitting of primitive Antilopini into gazelline and antidorcine branches. Derivation from the latter is consistent with the later ecological and morphological adaptations of caprines and alcelaphines. Furthermore, this sort of interpretation was implicit in Gentry's recognition of the alcelaphine affinities of *Aepyceros* which has clear antilopine rather than caprine origins.

Miocene antilopines tend to be much less highly differentiated than their descendants and it is difficult to find criteria in the very limited fragments that are available that will match up with the evolutionary trends that are clear enough in living tribes. Certainly teeth and horn cores, which are the main relics, can only provide the barest hints and clues: for instance hollow frontals, which are shared by Caprini and the antidorcine Antilopini.

The Caprini, together with their more archaic allies, the Rupicaprini and Ovibovini, do not flourish in the richer Eurasian habitats. They are replaced there by the cervids, (which have made ecological radiations comparable to those of some African bovids) and by the larger Bovini. Gazelles have tended to dominate the drier more open steppes from the Miocene onwards. Now restricted to more difficult environments, the Caprini have diversified and become highly specialized.

The fact that such vast areas of Eurasia are made up of long mountain chains tends to obscure the discontinuous "relic" pattern of caprine distribution. Their long representation in the fossil record and less specialized beginnings accords with this pattern. Their dietary and ecological adaptations have something in common with the antidorcine, alcelaphine and hippotragine lineages in that there tend to be strong seasonal variations in the quality of their food and catenary movements up and down often mountainous habitats are general.

Extensive mountain chains are mostly restricted to northern Africa where wild goats were once abundant. The less precipitous and varied tropical



The caprine world

uplands have been colonized by a wide assortment of indigenous bovids with the klipspringer coming closest to the caprines' specialized niche (see p. 174).

Caprine specialization has concerned diet less than habitat and morphology. Schaller (1977) has described the Caprini as generalized and flexible feeders living in habitats of simple structure where primary productivity is low, and he pointed out that their optimum size range is between 25 and 75 kg and they are often the only ruminants in their habitat; in other words, adaptable medium-sized animals with large niches in very simple habitats. This catholicity has particularly suited the goat for domestication. Introduced at high densities, it has been able to reduce more complex habitats to conditions resembling its original barren hillside environment;



it is not recommended in gardens. "Both sheep and goats evolved into their present forms during the turmoil of the ice age and both probably had the centre of their evolution in the mountains of Asia where alpine ungulates reached and maintained their greatest diversity" (Schaller, 1977). The emergence of sheep which are adapted to less precipitous ground and more of a grass diet than goats has been extensively discussed by Geist (1971a), who has remarked that the sheep of central Asia are of rather recent evolutionary origin, having "surged from unglaciated terrain into the mountain ranges after glacial withdrawal."

In spite of a poor fossil background the surviving species of Caprini, Ovibovini and Rupicaprini provide the picture of a distinct but limited evolutionary radiation that has been sensitively explored by Schaller (1977) who remarked "Although each species represents the end of a lineage adapted to a certain environment, it is valid to infer that morphologically

conservative forms may resemble the ancestral ones in appearance and behaviour."

For example, the chamois, *Rupicapra*, has many resemblances with the Antilopini in size, skull and tooth structure, diet, face and throat pattern. Males are seasonally territorial, at which time they chase off rivals and also attempt to control the movements of females within their territories. Rivals circle and make lateral displays flagging their throat patches and face markings in a similar manner to gazelles. In common with several other caprines and the impala, *Aepyceros*, they flash their tongue during courtship. Another rupicaprine, the serow, *Capricornis*, exhibits primitive antilopine traits in its small exclusive family groups and the possession of face glands. The Ovibovini have been described by Schaller as bulky rupicaprids which have evolved unsophisticated frontal methods of combat and he sees the true sheep and goats, *Ovis* and *Capra*, linked to the Rupicaprini by intermediate forms, the tahrs (*Hemitragus*) species. The well-horned female tahr are quite aggressive to one another; the males maintain small territories but only temporarily during the rut. Schaller has pointed out that there is a cline in sexual dimorphism which has a good correspondence with differing land tenure systems, increasing dimorphism in the horns of more advanced species correlating with increased emphasis on dominance hierarchies. This cline implies a slow evolutionary progression from territorial spacing, in which males possess small spiked horns, to dominance hierarchies in which the males have massive arches or spirals. The development of these horns is clearly related to increased male competition for females and Geist (1966b) has pointed out that the differences between territorial and hierarchical caprines involve basic physiological modifications in that successful males add to their status by prolonging body and especially horn growth beyond the ecological optimum. Thus a chamois matures in under three years, a big horn sheep in not less than six-and-a-half. Schaller not only sees the females representing the ecological optimum but also free from the selective pressures that have elaborated male physique and behaviour; he portrays them as actually reflecting a conservative rupicaprid ancestry in their physical type.

Schaffer and Reed (1972) correlated horn sizes with benign or harsh environments and they took survivorship as a measure of relative harshness. Geist (1971a) equated the frequency and intensity of ramming with horn size and the "quality" of a population. Schaller (1977) instead put emphasis on the size and structure of a population and remarked that the larger and more permanent a society the more often are members likely to find themselves in competitive situations. As in other bovids, higher population density seems to have been the major factor increasing competition between males. Higher levels of competition sustained over long periods of time are a more likely explanation than direct environmental factors for greater horn size in populations from optimal habitats.

The frontal sinus, which is present in all Caprini, Ovibovini and Rupicaprini, provides one of the pre-conditions for various elaborations of horn shape. Its extent correlates with skull shape and relative evolutionary advancement; the more primitive Rupicaprini having small sinuses over the front end of the brain case; more advanced Caprini extensive honeycomb

sinuses (their septa lying along the lines of principal stress) overlying most, if not all, of the cranial roof and filling the horn core stems (Schaffer and Reed, 1972). These authors distinguished between long-horned “clashers” (typified by goats, *Capra*) and thick-horned “rammers” or “bashers” (mostly species of sheep, *Ovis*). The former exchange blows far out on the horns, their long lever arms and a protruding braincase reduce rotary torque which is generated about the occiput and strong neck muscles are sufficient to absorb the dampened force of horn clashing. Advanced sheep instead have broader skulls and the whole neck and cranium form a column to absorb a higher force of impact. An intricate filigree of diploe and thin bony septa form an extensive bonnet over the cranial capsule (see illustration).

The functional efficiency of particular horn shapes, the quality of their design, finds some reflection in the relative frequency with which they are broken, and Schaller (1977) has quantified horn damage in different species and races. He adds that damage is probably also a measure of the frequency and intensity of clashing in particular populations. Frequent fractures are concrete evidence of the intense selection that has shaped caprid horns. As for the development of horn spirals, these were first analysed by Wentworth Thompson (1942). Pointing out that the horn elongates because of continual growth within the annulus at its base, he observed that if the rate of growth is identical on all sides of the annulus the horn grows straight, if it is greater on one side than on the other it becomes curved.

“If the maximal and minimal velocities of growth be precisely at opposite sides of the zone of growth, the resultant spiral will be a plane spiral; but if they be not precisely or diametrically opposite, then the spiral will be a gauche spiral in space ... in greater or lesser degree there is always superimposed upon the plane logarithmic spiral a helical spiral in space ... the constant angle of the logarithmic spiral is very much the same but the enveloping angle of the cone differs greatly” (*from species to species*). “Thus the long, drawn-out horns of *Ovis poli*, four feet or more from tip to tip, differ conspicuously from those of *Ovis ammon* or *Ovis hodgsoni*, in which a very similar logarithmic spiral is wound (as it were) round a much blunter cone.”

Wentworth Thompson could not resist a practical experiment. Noting that the transverse section of a typical ram's horn is triangular, he measured the length of three edges and came up with 80 cm along the outer edge, 74 cm along the inner and 45 cm along the posterior.

“Let us say that, roughly, they are in the ratio of 9:8:5. Then if we make a number of little cardboard triangles, equip each with three little legs (I make them of cork), whose relative lengths are as 9:8:5, and pile them up and stick them all together, we straightaway build up a curve of double curvature precisely analogous to the ram's horn.”

Form into Number—Wentworth Thompson had “plotted a curve” a three dimensional rate of growth no less than the plotter of a mortality table. Putting away his corks, his raw data, he stored a potential which is only being fully realized and applied to “modelling” very much larger problems in the age of the computer—Numbers into Form.



Appendix I

Conservation

When a close and aged relative dies the sense of loss is often intensified by regrets for the sentiments that never found expression, for opportunities of intercourse that were neglected and for questions that were never asked. In the tiny theatre of family life the cast is diminished, the prologue abbreviated and our own repertory is shallower, its character impoverished.

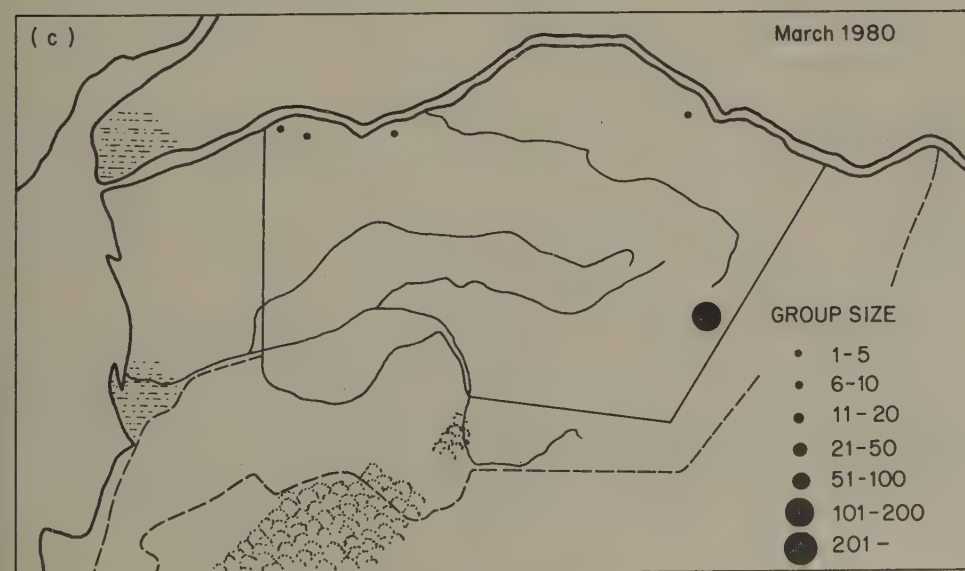
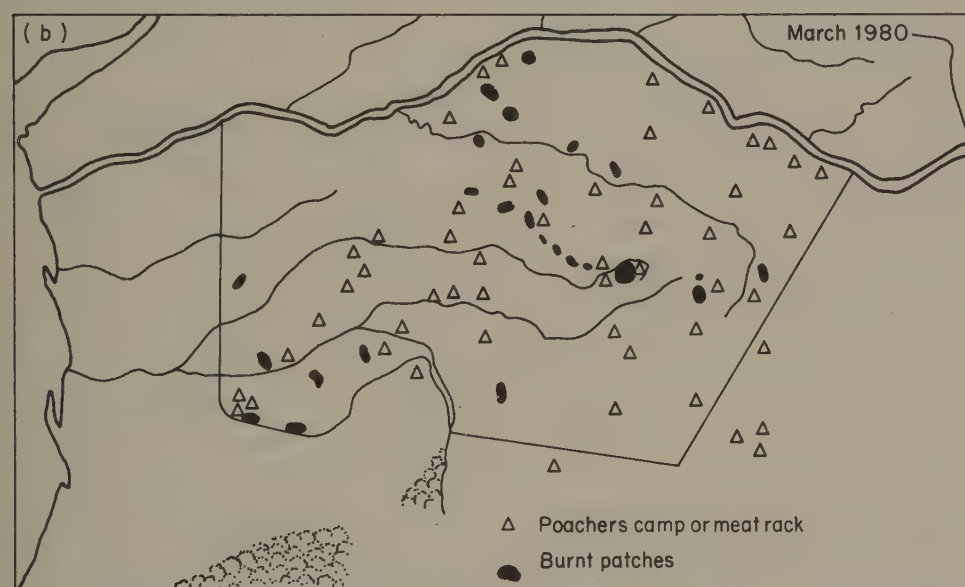
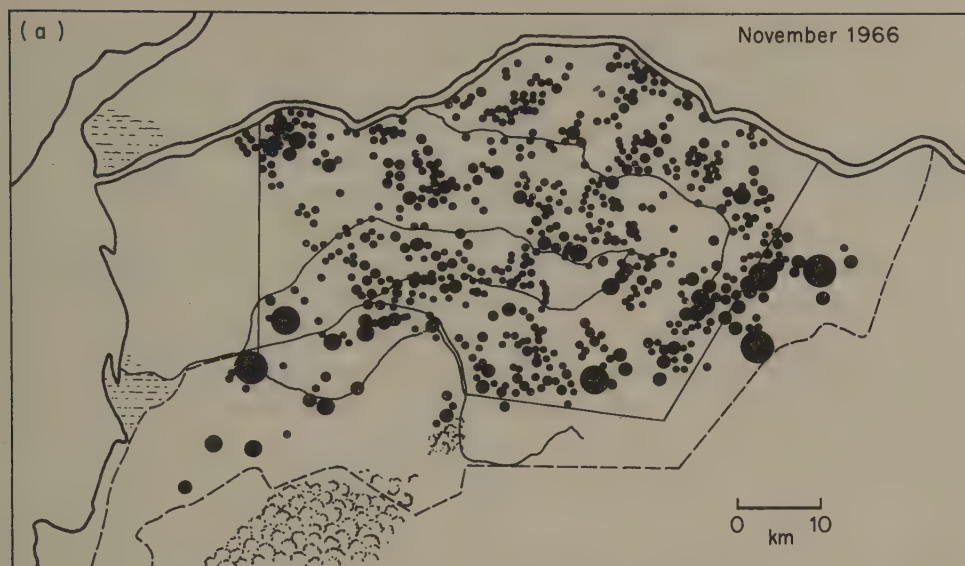
In the larger drama of human history and origins, staged in a global amphitheatre, dominated by mammalian evolution, we face devastating and unnecessary losses.

Just as we begin to evolve the ideas, fashion the methods and find the words to ask appropriate questions from a huge cast of actors they are poisoned off for gross and trivial motives.

It should not be supposed that the places, the habitats, the species described in these volumes needed to be destroyed out of human necessity. Highly diversified natural communities can live close to dense human settlements if the inhabitants have the will or the power to oppose the greedy few who would impoverish their natural heritage. Whereas technology can help us husband resources more economically (and might permit human densities higher than those current in parts of East Africa) the arrival and development of new techniques in Africa has more frequently encouraged a wasteful and exploitative expansion into wild lands. In innumerable cases fauna and flora have been extinguished out of greed, not need. The actors in our family drama have not died, they have been killed for the cents in their purses.

It is because mammals have been presented in an evolutionary context throughout these volumes that I stress familiarity, genetic relationship and historical drama. A rationale for conservation that is based on evolutionary thinking gives a high priority to preserving animals and plants as natural communities because they manifest the processes whereby the human race evolved and came to occupy this globe together with a vast but ultimately finite number of other interacting organisms. In eastern Africa the living (and fossil) fauna and flora have begun to contribute materially to a deeper understanding of the roots of our race and it is not without reason that this region has been called a cradle of mankind.

There are numerous corollaries for an evolutionary view of man and his environment but human survival and self-interest alone provide arguments for conservation without recourse to historical, philosophical or evolutionary invocations. The World Conservation Strategy 1980 (a policy guide aimed at Governments, Developers and others concerned with living resources) stressed three political objectives for conservation. The first was to maintain the ecological processes and life support systems essential to human survival and development. The second to preserve the genetic diversity on which the essential ecosystems depend. The third was to ensure that human exploitation of species and ecosystems could be sustained without permanently depleting living resources.



Elephants in North Bunyoro, Kaba-lega National Park in (a) 1966 and (b, c) 1980. From Malpas, 1980.

This document recognized that a major obstacle to conservation was the inability of individuals, governments and particularly the agents of development to perceive that ecological processes cut across all sectors of human enterprise and existence (a shortsightedness that is often deliberate). The World Conservation Strategy has not been the first to pin-point the vulnerability of rural areas in developing countries. These mainly tropical areas have suffered from a general inability to devise conservation-based development which is part of a wider failure of responsibility and a lack of will or ability to conserve. Resources are unlikely to be allocated in the balanced patterns appropriate to rational conservation so long as narrow short-term interests are the major preoccupation of practical politics and so long as inflexible and needlessly destructive technology is employed to force the pace of development.

Because of their cost and scale, large development schemes in Africa usually depend upon imported technology, foreign investment and advice. The political commitments of all participants generally prohibit environmental considerations being taken into account. There have been numerous more or less successful development schemes and several spectacular and dangerous failures. For example, the symbiotic land-use systems of some pastoral and agricultural peoples in the Sahelian zone were already well understood before they were destroyed by irrigation consultants from the U.N., groundnut growers and ranchers. Productivity declined as fences barred movement, groundnuts leached the soil and trees were felled. Amongst other functions these "Haraz" trees provided vital dry-season browse for livestock which manured the land for the next crop (Robertson, 1974). Such is the rivalry between aid-giving powers that quick propagandistic or political advantages tend to override all other considerations.

The Ankole-Masaka ranching scheme in Uganda illustrated this factor and also how thinly the benefits of development can be spread in an area that was once likened to Serengeti for its wildlife (Volume I, p. 36). Some \$650,000 of American aid was spent on 180,000 acres which were allocated to 57 ranchers (Montagne, 1971). This was part of a four million dollar loan agreement signed in 1966 which aimed to set up 100 or so ranches of several thousand acres each. In the tse-tse eradication campaign that preceded this project 44,000 mammals were shot in an area of 3,000 sq. km over a period of six years, woody vegetation was cleared and there was intensive spraying of insecticide to exterminate the flies. In spite of local criticism the scheme was never subjected to an ecological impact analysis. The financial and political investment was so massive that its implementors were able to excise and fence off land and watering points from the adjacent Game Reserve with impunity and without reference to the Wildlife Authorities who had proposed National Park status for this area. This reserve is now illegally overrun with cattle.

One can only wonder at the long-term consequences of external subsidy for a handful of ranchers in a region of peasant farmers. One of the originators of the techniques used to eradicate the tse-tse flies, Swynnerton (1936) considered large-scale intervention ineffective and unjustifiable if not followed by immediate and intensive agricultural settlement. He thought that only the promise of substantial economic and social benefits could

excuse such wholesale destruction of valuable animals and dismantling of indigenous ecosystems. All this is not to oppose development or not to recognize the incompatibility of dangerous or destructive animals with intensive agriculture but to oppose profligate waste.

The misuse of technology in settled times is multiplied in periods of chaos and in the ten years since Amin seized power brutalization of the people of Uganda has been accompanied by a huge onslaught on their precious wildlife, particularly in the last three or four years. The arms, ammunition and sophisticated transport and equipment of the military have provided the principal means of killing both people and animals. African armies are supplied with such equipment by USSR, USA, Britain, Czechoslovakia, France, Yugoslavia, China and others. The ivory and rhino-horns find ready markets in India, Japan, Hong Kong, Belgium, Singapore and the Middle East. Every major country in the world today contributes, directly or indirectly, towards destruction of the African environment, its flora and fauna.

In Uganda, Malpas (1980) has recorded that more than 30,000 elephants have been reduced to less than 2,000 in ten years (see Volume IIIB and margin maps). In Ajais Reserve, where the last white rhino have now been exterminated, six men with automatic rifles recently mobilized 400 villagers for a monster shooting drive while unarmed wildlife guards looked on helplessly.

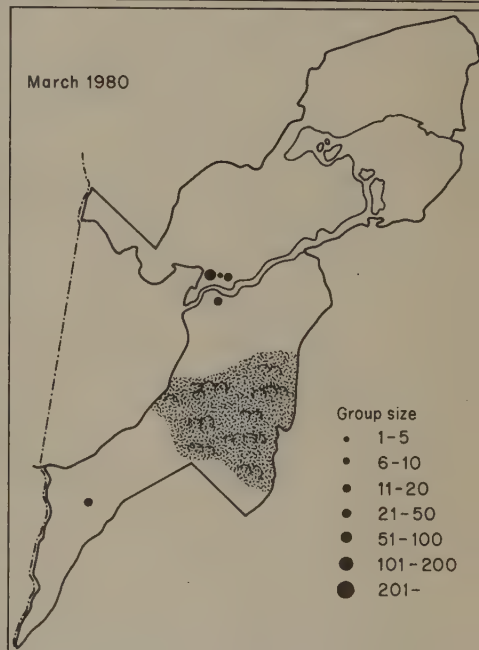
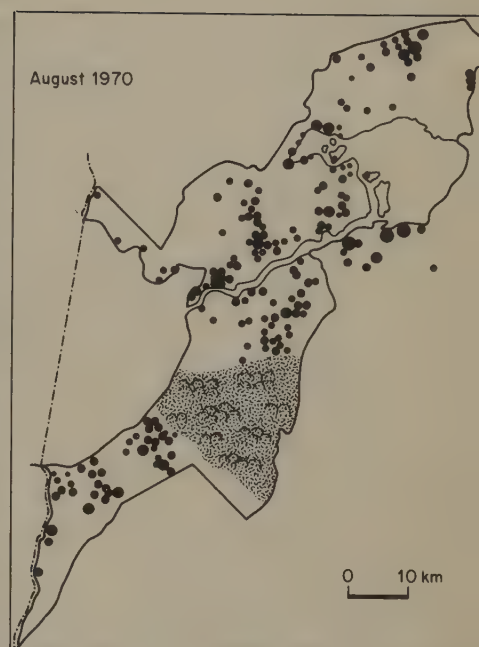
Human activity in Kigezi gorilla sanctuary has deterred the few gorillas left in this international frontier area from entering Uganda. The 100 odd gorillas in the Bwindi Reserve (one-third of the world population of *Pan g. beringei*, the rarest race of gorilla) have few young and cannot be expected to survive long under the present disturbed conditions. A 15-fold increase in logging activity has followed the building of a new road.

In Semliki Reserve, another proposed National Park, elephants and lelwel hartebeest have been exterminated and many other species decimated.

In the Ruwenzori National Park regulation of the once flourishing fisheries has been abandoned, a vast increase in fishing has been followed by a sharp decline in fish, the fishermen have turned to poaching hippos and other animals for meat, further depleting the nutrient cycle on which the fisheries are dependent (see Volume IIIB, p. 263), a 68–80% decline in hippo, buffalo and topi populations has been recorded in this park.

The actual and potential dimensions of loss have found some measure in the maps and text of the book. A minimum of 15 species are endangered and 75 species are rare or of very restricted range. East Africa should therefore be the scene for a special effort to conserve mammals. The region is certainly unique but it is also broadly representative of the continent as a whole. There are well over 400 species, 180 genera, 47 families and 12 orders (by contrast western Europe has less than 200 species belonging to 27 families and only 8 orders. Biologists, naturalists, indeed anyone with biological insight will appreciate the extraordinary wealth and biogeographical significance of East Africa.

Because of this awareness interested scientists and naturalists, wherever they are, must share with the peoples of East Africa a direct responsibility for ensuring the survival of natural biological communities in this region.



Elephants in Ruwenzori National Park in 1970 and 1980. From Malpas, 1980.

To appreciate the unique and finite nature of eastern Africa's fauna and flora perspectives of time and geography are needed which are not easy to acquire at the local level (for example very few East Africans will ever read these pages). There is, however, a scattering of individuals and institutions devoted to conservation in East Africa and the outstanding success of Wildlife Clubs in Kenya schools has demonstrated what funds of enthusiasm for natural history exist in our youth.

There are very few countries where political leaders share such enthusiasms. The caution, careful assessments and restrictions of human activities that tend to be urged by conservationists are usually anathema to the ambitious politician with his short-term aims and dependence upon power-bases with local or industrial vested interests. Governments commonly give expression to these values. For example, the Third Report of the Countryside Commission in Great Britain (1970) stated that there was little evidence of the British Government's intention to afford conservation the consideration it should receive. Official neglect and official values find their expression in the few conspicuous items of expenditure within what are euphemistically called National Parks in England—power lines, water reservoirs, unsightly public lavatories and prohibition signs.

In contrast, the East African Governments' record, particularly in founding and maintaining their magnificent National Parks, cannot be matched anywhere in the world. The considerable achievements of conservation in East Africa have depended upon the support of a few exceptional leaders who have often swum against the political tide. It is generally easier for decision-makers to neglect or ignore proposals which have a philosophy, objectives, perspectives of time and land-use that are outside their own frame of reference.

The inability to conceive of conservation as an active, demanding responsibility may lie behind the disturbing reports of the Kenya Auditor General which show that over three recent years the Ministry of Tourism and Wildlife has turned over some £5,000,000 (\$10,000,000) unspent to central government. There has also been a neglect of opportunities for external finance for conservation by Tanzania. What a sad irony that while its two neighbours ignored such resources the hard-pressed Wildlife Departments in Amin's Uganda were often unable to clothe, arm, transport or even pay their long-suffering staff.

Malpas (1980) has written:

"The Uganda people are at present recovering from a very difficult period in their history and they face innumerable day-to-day problems. It is difficult for an outsider to understand the scale of these hardships. It should be understood, therefore, that the ordinary Ugandan does not, at present, place the preservation of the country's wildlife high on his list of priorities. To a large extent, however, this is due to the lack of knowledge of the parks and reserves and of their potential benefits. Most villagers in areas adjoining the protected regions are unaware of the massive decline in wildlife abundance in recent years and would certainly be surprised to learn that elephant are in danger of extinction. Yet it is these people who have the power to halt the decline. A programme is urgently required to educate the people to the value of Uganda's wildlife heritage."

It will be on efforts of contemporary biologists and conservationists that such a programme will depend.

Over the past two decades a handful of lucky or resourceful scientists have had the privilege of working in a superb natural laboratory. They have had its use with few responsibilities and practically no financial liability for its maintenance. Some workers from overseas have had a significant local impact and have generated an interest in conservation with the special virtue of being focused on particular places. Such scientists have come from institutions with well-defined scientific, educational or cultural objectives and have worked on sustained long-term projects in close partnership with local bodies such as government departments (wildlife, forestry) universities, schools, clubs, cooperatives, firms or individual land-owners, scientists or naturalists. Some notable partnerships have been forged—Frankfurt Zoological Society and the Serengeti Research Institute, the New York Zoological Society and Amboseli National Park; Tsavo National Park and the Animal Ecology Research Group, Oxford; the Uganda Forest Department in Toro and Rockefeller University. Much more could be done if biologists and their institutions in the developed world would show the initiative. It is a sad reflexion on the state of contemporary biology that its practitioners seldom recognize their opportunities or their responsibilities.

It is government and local leadership that ultimately determine the fate of natural communities. Practical conservation must work with and through the numerous branches of national and local authorities, focusing on specific communities in particular places. Splendid national parks embracing thousands of square kilometres have been established by the East African governments on the instigation of several generations of far-sighted individuals. As populations expand and with them agricultural and urban development, the emphasis alters. There is now less scope for large new parks in wilderness areas but there is an increasing need for upgrading many of the smaller sanctuaries and reserves that are scattered across the length and breadth of East Africa and gazetted some new ones. Often these are or very soon will be within well-populated areas and I consider that it will be the survival of numerous unique natural communities beside dense human populations that will pose the major challenge to conservation in the future.

It is in small countryside sanctuaries that people have the chance of developing an appreciation for the detailed fabric of their environment and it is at this very local level that people may recognize responsibilities to generations yet unborn. Experience has shown that sanctuaries in such places are sometimes tended with conscientious pride by their wards. It should be added that the position and standing of conservationists in rural areas can be materially reinforced when knowledgeable and friendly visitors have come great distances to participate in studies, share their knowledge and publicize their joint efforts.

Ultimately effective conservation must depend upon local enthusiasm and good will and this is contingent upon the social and personal values of East Africans. These may be increasingly influenced by the scientific, cultural, and aesthetic considerations that underlie the conservation move-

ment in other countries but they are also subject to the more powerful bait of money.

In an address to the Uganda Society in 1973 I reminded my audience of the pivotal role of value-systems in conservation and suggested that biological book-keeping and accountancy were long overdue.

"The simplest means of measuring biological richness is, of course, compiling lists of species, genera, families and higher taxons. However, in assessing the richness of a biological community living in a circumscribed area I think the elaboration of a point system is possible. Following the initial assessment of species there should be a further examination of the overall distribution of each species to determine its relative rarity and further points should be given to each species with a restricted range. Still further points could be awarded to species that are exceptionally vulnerable for any reason. Local endemics would, of course, get the highest points.

Biological knowledge of eastern Africa has advanced to the point where this exercise could be done reasonably well for popular groups like orchids, birds and mammals and perhaps also for butterflies, amphibians, reptiles and trees.

Economic values are today considered by the majority to be the ultimate criterion of policy and the forces working against conservation derive their power from this assumption. The economic factor has been described as if it were the third of a Trinity with God and Satan. There is no gainsaying the contention that no commercial value can be put upon the great majority of species that the conservationist wishes to preserve but since the confrontation is as much a conflict of values is it not possible that supra-economic values should appeal to local susceptibilities and value systems?

Measuring wealth is important, because *feeling* wealthy is probably as significant for most people as actually *being* wealthy and I think that officials, game wardens, foresters and politicians might take more pride in their responsibilities to conservation if they were provided with data that showed them in simple numerical terms what 'biological millionaires' their countries are. In addition to such an appeal to pride, status and responsibility it should be remembered that there has been in some parts of Africa a tradition of social responsibility in relation to the land where a man saw himself as a mere link in a long chain of life extending way back into the past and on into the unforeseeable future. Aldo Leopold's statement on ethics and ecology might make particularly good sense within this tradition—'That land is a community is the basic concept of ecology, but that land is to be loved and respected is an extension of ethics . . . we abuse land because we regard it as a commodity belonging to us. When we see land as a community to which we belong we may begin to use it with love and respect.'

Returning to the measurable units of value, the species, it must be remembered that the economist can never put a value on a species. All he can do is recognize that a species (or the biological community of which it is a part) is unique and irreplaceable. So what value can we put on a unique form of life?

A species is the realization of a unique possibility of existence. Our own collective existence as the human race is but one single possibility of existence and each single species is a manifestation of *other* potentialities. The destruction of a species represents the loss within the universe, for all time, of one unique potentiality in life. It is also the betrayal of an ancient trust linking our ancestors with our descendants. It is irresponsible impoverishment of our already poor planet."

The forests of eastern Africa are among the most vulnerable because they are small and isolated. They also represent ancient biotic communities offering the largest range of niches to forms of life. The risk of impoverish-

ment rises when the community that is threatened is rich in species but small in areas. This is certainly the case in East Africa where a fraction of the land is true forest. It is now generally recognized that biological productivity and ecological wealth and versatility depend upon a wide variety of species, which allow flexibility within the ecosystem. Impoverished ecosystems lose their equilibrium, may be easily invaded by foreign species and lose productivity.

The botanist Edward Ayensu has pointed out that nearly all important food and cash crops in Africa are imported species. Some, such as corn, have only been established in the last 50 years. With about 40,000 species of indigenous flora (a high proportion of which are forest species) Africa faces a large-scale loss of genetic diversity; "suppose" asks Ayensu, "the progenitors of corn had been wiped out carelessly?"

In asserting the intrinsic biological value of some of the indigenous communities that remain, thoughtful and concerned foresters have sometimes had the ground cut away from under their feet by the activities and attitudes of officials or teachers within their own departments. For example, British aid technicians have toured East African countries in recent years promoting large-scale mobile charcoal-burning techniques. In energetic and very successful campaigns they have deliberately inculcated the simplistic concept that forests are worthless unless exploited for profit. Such technicians have surely overstepped their brief. The forester Dawkins (1963) saw the justification of a forest's existence on material production alone as futile when encroachment by metals, cement, synthetics or even changing customs could destroy the argument. In Dawkin's view the cultural benefits have a far longer foreseeable future than the productive.

The uncontrolled and damaging techniques of timber-extractors in Africa would generally be unacceptable in the consumers' own countries and Ayensu has stressed the technical incompetence, ecological ignorance and general irresponsibility that has accompanied the devastation of Africa's forests. In temperate regions soil is the main repository of nutrient wealth. In moist tropical forests the thin layer of soil is relatively poor and nutrients are primarily retained in the vegetation itself. It should be no surprise that forests fail to regenerate when the nutrients have gone up in smoke or are carried away. Pointing to recent documentation of the destruction of some eight million square kilometres of tropical forest over the last century and a half and to the tepid attention given to the World Conservation Strategy, Ayensu has castigated journalists and the media for their concentration on ephemera and their disinterest and irresponsibility towards issues of environmental concern.

At this point we might return to the subject of who holds the ultimate responsibility for allowing the destruction of species. In traditional religions divine permission or sanction was generally recognized. For example, there is a long text in Genesis which can be read as a crude form of licence issued to Adam and his progeny. Today we are conscious of bearing the responsibility on our own shoulders. No one can escape some measure of the blame for the destruction of our heritage and we may well earn the reproaches, contempt, even curses of our grandchildren. Our generation now decides on the survival or destruction of other forms of life on this

planet and we have a special responsibility towards the unit of value we call the species, because we have only just begun to appreciate that these species only live or grow in certain strictly limited spots. This is especially true for East Africa's "island" communities. Considering how fundamental knowledge has been gleaned from the intensive study of homely things like sweet peas, honey bees and fruit flies, how much remains to be learnt, particularly in Africa. The lack of knowledge of the tropical flora and fauna of Africa is a reproach to twentieth century man and to his science.

"Science enlarges our vision and ecology is concerned with cause and consequences on a broad front. We should be delving ecologically into the future but in general we are not doing so." (Darling, 1970).

It is important to remember the zoogeographic pattern which suggests that some areas are ancient relic refuges while other areas have been more recently colonized by widespread and common dominant species. This pattern reveals that not all species nor all areas of forest are of equal value. Some very small East African forests possess special unique endemics; others possess an incredibly rich variety of rare species and these small areas are often superior in number of species (and "conservation points") to those vast forests of Canada, Scandinavia and Russia, indeed they may actually constitute some of the greatest concentrations of vertebrate species known on earth.

I consider that a mosaic of sanctuaries (some of them relatively small), all over the country is the ultimate means of preserving representative habitats and giving them a value. Most would need to be under the supervision of a governmental environmental department but could often be loosely attached to educational or other agencies.

The determination of the areas which should be conserved would operate at different levels. The first would be the overall national level and here we find some of the appropriate measures are under consideration or have already been attempted. This level of planning embraces the preservation of communities and species of special or unique value such as local endemics, afro-alpine habitats and spectacular rarities such as gorillas, yellow-backed duikers and white rhinos.

A second level operates within the large game of forest reserves where activities such as pastoralism, logging and tree poisoning might be a threat to the survival of particular biological communities or species. Some reserves need to be rated a higher or lower conservation value and the mosaic of small sanctuaries that I believe is essential should be computed accordingly.

The size and the frequency of the sanctuaries should take account of the overall value of the area and in important reserves should be determined by certain parameters such as vegetation types (ensuring that every type is represented) catenas (with drainage and altitudinal zones or belts included) and rotations (where cycles can be recognized there should be a provision for the operation and study of this dynamic element in appropriate strips and protected zones.)

The average percentage of area given over to mosaic sanctuaries in indigenous vegetation reserves might average out at about ten per cent. In areas of peripheral interest or importance this could be diminished, while

in very important faunal and floral refuge areas it should be greater.

Looking forward into the not-so-distant future it is not impossible to see legislation obliging large-scale developers, be they open-cast miners, oil-men, sugar growers, ranchers, tea planters or timber mills to devote ten per cent of their allocated area of exploitation to sanctuaries for the original fauna and flora of the region or an equivalent of their profits to finance external sanctuaries. Fraser-Darling has already suggested the taxing of those who create ecological dereliction as restitution for their ravages. Foreign governments the buyers and consumers of timber, sugar, coffee and tea should also pay to offset the terrible ecological cost that their endless appetite engenders.

When men are obliged to live in the midst of wide areas totally given over to monocultures or to industrial deserts we can already see the cultural, spiritual if not physical poverty of these unfortunate people.

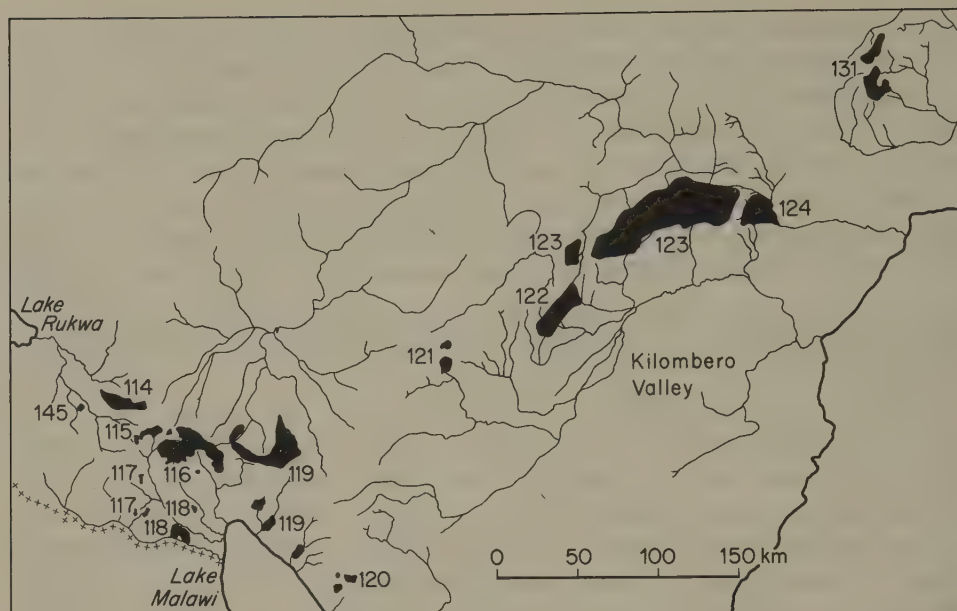
In this biological treasure house the future tithing of large-scale consumers and enterprises might be one way of making development directly responsible for these supra-economic values that its activities threaten.

Since the Stockholm conference and foundation of the United Nations Environmental Programme in Nairobi conservation has gained momentum in East Africa and a less diffident approach to environmental issues is emerging. For example, at one meeting environmentalists drew up plans for calling polluting industries to account by means of tribunals. These will collect data on pollution, describe its effects, identify culprits and outline programmes of corrective legislation. Wholesale destroyers of valuable ecosystems should be equally subject to such investigation and discipline. By such means the beneficiaries from environmental abuse and exploitation might be made more accountable to the public and to future generations.

Conservation and the environment has also become an increasingly transnational concern. The World Conservation Strategy has called for a complete network of protected representative samples of ecosystems in which national programmes are coordinated with international efforts. The Strategy has also published, as part of its requirements in maintaining genetic diversity, a priority formulation for the prevention of extinctions. Such international initiatives will have limited chances of being implemented without the active support of individual naturalists focusing their energies on particular places and species, and it is at this ground level that all those with an interest in conservation can play a part.

The conservation of mammals is but one aspect of conservation in eastern Africa but I hope this inventory and atlas of species will help to focus efforts. There are already several unique communities and rare endemics that need more effective protection if they are to survive. For example, a recent change in the dietary habits of salary-earners in the cities is one of the new developments that now threatens the small remnant forests of Tanzania. At 400 shillings a bag, the price of potatoes in Dar-es-Salaam and other towns has been sufficient to finance a continuous lorry trade between remote uplands, where potatoes grow well and the coast, where they are consumed. Hard working Hehe women are slashing and burning the remaining forests of the Uzungwa scrap (where the fauna and flora

Forest relics in the southern highlands, Tanzania. See pp. 606 and 607 for Key.



are still incompletely known but which shelter many important endemic forms).

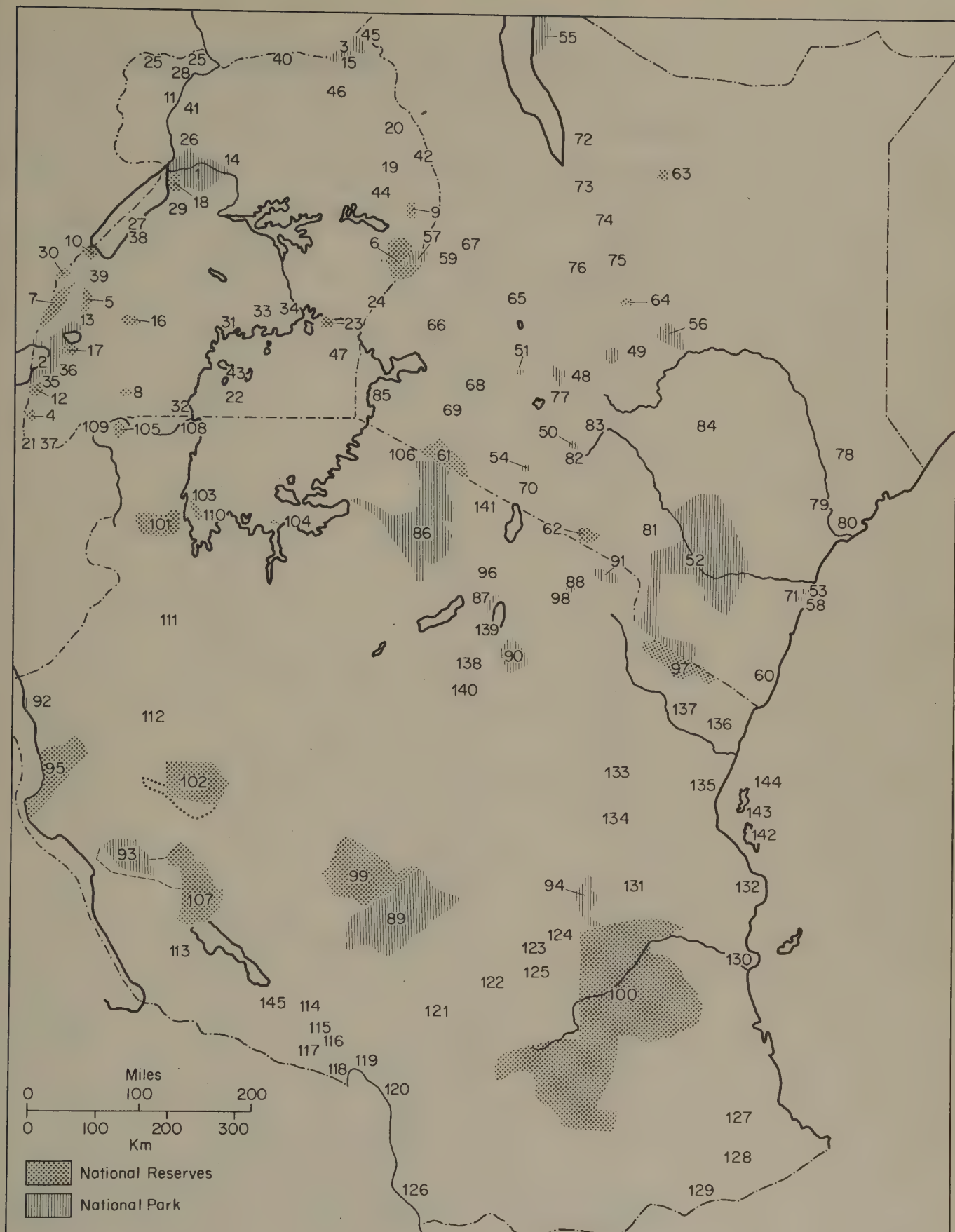
In the Usambaras, charcoal-burning and cardamom-growing has caused large-scale illegal destruction of the remaining indigenous forests (margin map).

All over Tanzania the felling of forests in montane areas is causing the drying out of what were once permanent rivers, with incalculable dangers for downstream areas in the form of flash floods and dry-season droughts, i.e. the Yaida and other rivers in Mbulu, the Tumwisi River in Ileje, the Rau and other rivers on Kilimanjaro.

The map on p. 603 indicates many of the major faunal localities and biological reserves in East Africa. These localities are listed on p. 604 with their current land-use, status and a provisional priority rating based upon a composite assessment of their ecological significance.



Destruction of forest in West Usambara. From Van Willigen, 1980



CONSERVATION AREAS IN EAST AFRICA

Uganda

	CURRENT STATUS	LOCALITY NAME	SIZE	RATING
1	N.P.	Kabalega (Murchison) Falls	A (3,900)	*****
2	N.P.	Ruwenzori (Queen Elizabeth)	A (1,979)	*****
3	N.P.	Kidepo	A (1,400)	***
4	P.N.P. (F.R.)	Bwindi (Impenetrable) Forest	B (297)	*****
5	P.N.P. (F.R.)	Kibale Forest	B (400)	*****
6	P.N.P. (F.R.)	Mount Elgon	B (860)	*****
7	P.N.P. (F.R.)	Ruwenzori Mountains	A (1,300)	*****
8	P.N.P. (N.R.)	Lake Mburo	B (542)	***
9	P.N.P. (F.R.)	Kadam/Debasien	A (440)	***
10	P.N.P. (N.R.)	Semliki (Toro)	B (554)	***
11	P.N.P. (N.R.)	Ajai's Island (Inde)	B (158)	*
12	P.N.P. (N.R.)	Kigezi	B (332)	**
13	P.N.P. (F.R. + N.R.)	Kibale Corridor	B (343)	**
14	P.N.P. (F.R. + N.R.)	Kaniyo-Papidi/Karuma	B (720)	**
15	P.N.P. (F.R.)	Marangole	B	**
16	N.R.	Katonga	B (209)	**
17	N.R.	Kyambura	B (155)	**
18	N.R.	Bugungu	B (518)	*
19	N.R.	Bokora	A	**
20	N.R.	Matheniko	A	**
21	D.S.	Bufumbira Gorilla Sanctuary	C (48)	*****
22	D.S.	Nkosi Sitatunga Sanctuary	C	**
23	P.N.P. (F.R.)	South Busoga	C	*
24	D.S.	Malawa	C	*
25	F.R./D.S.	Mt Kei, Otze, Dufie	B	**
26	N.R./L.C.A.	Aswa Lolim†	B	**
27	L.C.A.	Kaiso-Tonya	B (230)	**
28	U.F.A.	Lomunga/Waka	B	**
29	F.R.	Budongo/Siba	B	**
30	F.R.	Bwamba	B (219)	*****
31	F.R.	Mpanga	C	**
32	F.R.	Sango Bay	B	*****
33	F.R.	Kifu/Mukono	C	*
34	F.R.	Mabira	B	**
35	F.R.	Maramagambo/Kalinzu	B (280)	*****
36	F.R.	Kashohya-Kitomi	B	*****
37	F.R.	Echuya	C	*****
38	F.R.	Bugoma	B	**
39	F.R.	Itwara	B	*****
40	F.R.	Agoro/Imatong	B	**
41	F.R.	Ainge/Kilak	B	*
42	F.R.	Moroto	B	*
43	F.R.	Towa (Ssesse)	C	*
44	F.R.	Napak (Kamalinga)	B	*

† Arbitrarily degazetted by Idi Amin. This important area should be returned to National Reserve status.

CURRENT STATUS		LOCALITY NAME	SIZE	RATING
45	F.R.	Zulia	A	*
46	F.R.	Orom	B	*
47	U.F.A.	Lolui Island	C	**
Kenya				
48	N.P.	Aberdare	B (766)	*****
49	N.P.	Mt Kenya	B (715)	*****
50	N.P.	Nairobi	B(117)	***
51	N.P.	Lake Nakuru	B (57)	***
52	N.P.	Tsavo + Naai Ndethya N.R., + Kitui N.R., + Thua N.R., + Railway N.R.	A (20,812)	***
53	N.P.	Gedi	C (5.0)	**
54	N.P.	Ologesailie	C (0.2)	**
55	N.P.	Sibilo	A (1,570)	*****
56	N.P. + N.R.	Meru + Koru + Rahole N.R. + 4,320)	B(A) (870 + 4,320)	***
57	N.P.	Mt Elgon	B (169)	***
58	N.P./N.R.	Mal.-Watamu/Mida Creek + Marine N.P., + N.R., + Kisite/Mpunguni + Kiunga	B (213)	***
59	N.P.	Saiwa Swamp	C (1.9)	***
60	P.N.P. (N.R.)	Shimba Hills	B (192)	***
61	N.R.	Masai Mara	B (1,672)	***
62	N.P.	Amboseli	B (392)	***
63	P.N.P. (N.R.)	Marsabit	B (2,087 + 606 + 239 + 339)	***
64	N.R.	Samburo-Isiolo + Bisinadi N.R., + Shaba N.R., + Buffalo Springs	B (298)	***
65	N.R.	Lake Baringo Bogoria	C (107)	*
66	F.R.	Kakamega/Nandi Forests	B	***
67	F.R. (N.R.)	Kongelai/Cherengani + Nasolot N.R. + S. Turkana N.R.)	(925 + 1,091)	*
68	F.R.	Mau	B	***
69	F.R.	Chepalunga	C	*
70	U.F.A.	Lake Magadi	C	**
71	F.R.	Sokoke/Arabuko	B	*****
72	F.R.	Mt Kulal	C	**
73	F.R.	Mt Nyiru	B	***
74	F.R.	Ndoto Mts	B	*
75	N.R.	Losai N.R.	A (1,806)	*
76	P.S.	Leroghi Plateau	B	***
77	F.R.	Aberdare/Kinangop Forests	B	***
78	N.R.	Arawale	B (533)	****
79	N.R.	Tana River Primate Swamp Forests	B (165)	****
80	F.R. + N.R.	Witu Forest + Boni + Dodori N.R.	C + A (977 + 1,339)	***

	CURRENT STATUS	LOCALITY NAME	SIZE	RATING
81	F.R.	Kibwezi	C	*
82	D.S.	Kitengela	B	***
83	N.P.	Ol Doinyo Sapuk + Mwea N.R.	C (18 + 68)	**
84	F.R.	Ngamba	C	*
85	P.S.	Lambwe Valley	B (308)	*

Tanzania

86	P.N.P. (N.R.)	Serengeti (satellite area Maswa N.R.)	A (14,600)	*****
87	N.P.	Lake Manyara	B (228)	***
88	N.P.	Nigurdoto Crater	B (137)	****
89	N.P.	Ruaha	A (12,950)	***
90	N.P.	Tarangire	A (2,600)	***
91	N.P.	Kilimanjaro	B (755)	*****
92	N.P.	Gombe Stream	B (52)	***
93	N.P.	Katavi	A (2,253)	****
94	N.P.	Mikumi	A (3,230)	***
95	P.N.P. (F.R.)	Mahare/Kungwe Bay/Uvinza	A	*****
96	L.C.A.	Ngorongoro Conservation Unit	A	***
97	N.R.	Mkomazi/Umba	A	*
98	F.R.	Mt Meru	B	*
99	N.R.	Rungwa/Kizigo	A	***
100	N.R.	Selous	A	***
101	P.N.P. (N.R.)	Biharamulo Burigi	A	***
102	N.R.	Ugalla River	A	***
103	P.N.P. (N.R.)	Rubondo Island	B (259)	**
104	N.R.	Saanane Island	C	*
105	N.R.	Rumanyika Orugundu	B	**
106	N.R.	Lamai Wedge	B	*
107	N.R.	Rukwa (Uwanda N.R.)	A	***
108	F.R.	Minziro	B	****
109	N.R.	Ibanda Arena	B	***
110	F.R.	Maisome Island	B	**
111	P.S.	Nikonga River + Kigosi	B	***
112	P.S.	Malagarasi Swamps (Gombe) C.A.	B	***
113	P.D.S. (F.R.)	Sumbawanga (Mbizi) + Lyambo Hill	C	****
114	F.R.	Mbeya Range	B	*
115	F.R.	Umalila/Poroto Ridge (Ishinga + Lumwe Valley)	B	****
116	F.R.	Rungwe Mountain	B	****
117	L.C.A.	Kyosa/Muswima/Iyondo (Uplands)	C	***
118	F.R.	Masukulo, Kabulo (Lowlands) Livingstone-Kipengere Complex	C	***
119	F.R.	Njirikiru, Luponde, Silupati	C	****
120	F.R.	Sakaranyumo, Madenge Uzungwa-Kilombero Scarp Complex	C	****
121	E.R.	Kigogo Mufindi	C	*
122	F.R.	Uzungwa, Mwanihana, Ihange	B	***

CURRENT STATUS	LOCALITY NAME	SIZE	RATING
123 F.R.	Ikwambi Chita, Dabaga, Ukwega	B	***
124 P.D.S. (F.R.)	Magombera	B	*****
125 L.C.A.	Kilombero	A	*
126 F.R.	Matengo Hills, Liwiri-Kiteza/ Lwekea	C	****
127 F.R.	Rondo	B	***
128 L.C.A.	Chilangala	C	*
129 F.R.	Mbangala	B	*
130 F.R.	Rufigi Delta	B	**
131 F.R.	Uluguru (North and South Reserves)	B	*****
132 F.R.	Kazimzumburi	C	*
133 F.R.	North Ngurus	B	***
134 F.R.	South Ngurus	B	***
135 N.R., F.R.	Saadani Genda Genda	C	*
136 F.R.	East Usambaras	C	***
137 F.R.	West Usambaras	C	*****
138 F.R.	Nou	B	*
139 F.R.	Marang	B	*
140 F.R.	Hanang	C	***
141 F.R. + L.C.A.	Loliondo	B	*
142 D.S.	Jozani (Zanzibar)	C	*****
143 P.D.S. (F.R. + U.F.A.)	Uzi, Muyuni (Zanzibar)	C	*****
144 U.F.A.	Matanga, Mgogoni (Pemba)	C	***
145 U.F.A.	Songwe bat caves		*****

KEY TO CURRENT CONSERVATION STATUS

N.P. = National Park D.S. = Designated Sanctuary
N.R. = National Reserve F.R. = Forest Reserve
L.C.A. = Locally controlled conservation area

Prefix P. (Proposed) = Upgrading under consideration (current status in brackets)
U.F.A. = Ungazetted faunal areas

NOTE Only Forest Reserves of faunal significance are listed. Plantations or natural forests subject to very intensive silviculture are not listed and should not be designated as "Reserves".

SIZE A = large (over 900 sq. km) B = medium (50—900 sq. km)
C = small (less than 50 sq. km)

RATING 5 stars = Of highest biological significance
4 stars = Contains rare endemic species or communities
3 stars = Important representative eco-system
2 stars = Special scientific and cultural interest
1 star = Representative local reserve or remnant habitat

NOTE Ratings change, as when endangered species become extinct (i.e. Ajais rhino sanctuary dropped from 4 stars to 1) and as widely distributed species and communities become more restricted. In the latter case units in lower-categories may move into 4 and 5-star status. Higher ratings of forests and mountains reflect larger numbers of species and presence of endemic or relict species. It should be stressed that all conservation areas listed here are of substantial biological importance I have personally visited 105 of the localities listed.

Appendix II

Many of the mammals described in these volumes are of considerable economic value, particularly when they are subjects of research or zoo exhibits. Others are of critical significance for veterinary, medical or agricultural research. It is therefore important that up-to-date knowledge on their management be disseminated as widely as possible.

The development of immobilization and other drugs, radio-telemetry, scientific studies on physiology and nutrition, the manufacture of balanced dietary products and the design of management facilities have combined to transform the management of mammals at all levels. This is not as well appreciated as it should be, especially in Eastern Africa.

Workers in the field, in parks, zoos and research institutes can now monitor an animal's movements, activity and physiology. They can investigate its condition and attend to most aspects of its welfare on a routine basis.

The following notes have been specially compiled by David Jones, chief veterinary officer at the Zoological Society of London.

Management of Mammals in Captivity

David M. Jones

These notes are designed to provide a summary of some of the latest information particularly on the nutrition and handling of mammals with comments on their general management in captivity where applicable

Primates (Vol. I pp. 99-327)

African primates are well represented in captivity and with the possible exception of the leaf eaters are relatively easy to maintain. Most of those now exhibited in the major collections have been born in captivity and a considerable surplus of many species, especially baboons, patas and vervet monkeys are produced every year. Even the lowland gorilla which at one time was thought to be extremely difficult to keep and breed is doing well and there is likely to be a somewhat difficult situation shortly when the surplus produced cannot be accommodated by existing breeding centres.

At the time when large numbers of primates were being trapped and

exported, often through a series of dealers, the losses, both at the time of capture and during the process of shipment and acclimatization, were enormous. Animals were inadequately housed and fed, they often came into captivity injured in some way and frequently contracted a variety of human diseases in the holding camps. At one time young apes especially were frequently given human blood serum in the belief that this would passively protect them from human ailments. Instead, it often turned out to be a source of human pathogens, notably viral hepatitis.

All the primates are omnivorous to some degree (see profiles) but colobus monkeys and gorillas are almost exclusively plant eaters (see Vol. I pp. 119, 155, 163). In captivity considerable problems arise if primates are fed a completely vegetarian diet. In the wild a "folivore" or "frugivore" can select from a wide variety of plant species at different stages of growth. The material is fresh and as a consequence an adequate balance of nutrients is ingested. The available vegetable foods in captivity are most unlikely to provide this balance and it is much easier to give proteins of a high biological value in another form. A number of laboratory primate diets are now made in most developed countries and are usually available with two different crude protein levels (often 16—18% and 23—25%). Those with a higher protein level are also usually supplemented with a higher level of vitamins. These diets are often marketed in an expanded ("aerated") form which makes them more palatable and the pellets are available in a number of sizes.

On the whole, the apes, baboons, mangabeys and guenons take these pellets readily. The prosimians will usually take small quantities but the colobus monkeys may not take them at all. If a particular group of animals takes the pellet well, it is usually only necessary to feed the low protein form, giving it at a level of about 50—60% of the dry weight of the diet. If pellets are scattered around the enclosure, the animals have to actively search for them and all the members of the group have an opportunity to obtain enough. The best way to use pellets is to give them as the first feed of the day on their own. Once they have been eaten, the rest of the food which might consist of a wide variety of fruits, vegetables, cereals and seeds can be given. Although the vitamin C in these pellets is usually stabilized in manufacture, the diet may have been stored for some time and it is therefore good practice to provide this vitamin either by using adequate citrus fruits in the supplementary foods or by giving paediatric drops or tablets containing the vitamin on a daily basis.

Apart from pelleted diets, trials have been undertaken recently on powdered "complete" diets which, with the addition of water, set to a firm jelly. Many different flavours can be added to these and they appear to be very palatable to primates. Despite the research work that has been carried out on suitable diets for primates in captivity over the last 20 years, poor growth rates and a chronic wasting syndrome often coupled with nutritional bone disease are still seen where owners have been attempting to maintain their animals on the traditional "fruit and vegetable salads" alone. Protein, calcium, phosphorus and vitamin D₃ are absent from such diets in any quantity and must be provided if these problems are to be avoided.

If primates will not take any of the commercially available diets, even

smaller quantities of the higher protein forms, a number of other possibilities can be tried to ensure that the animals' intake is balanced. Cheese and milk are often readily taken and mincemeat or tinned meats in small quantities are also satisfactory but may need to be supplemented with calcium and phosphorus. Small primates in particular will take cultured invertebrates such as mealworms and locusts but these also need to be supplemented, especially with calcium. High protein baby foods, usually based on milk powder, are available in various flavours and are usually very palatable.

Water, which can be given to most mammals in open containers, is best provided to primates through automatic drip feeders with steel nozzles. This is mainly because any other form of water container is usually readily overturned and then frequently used as a toy.

In captivity, primates are often not as gregarious as may appear to be the case in the wild. Most successful groups begin with relatively small numbers of young animals. Although it is possible to begin with six or eight young baboons or vervet monkeys, all of which are introduced to a new enclosure at the same time, the colobus monkeys, most of the guenons and the prosimians do better if they are allowed to build up from a pair or at most a male and two females. It is often impossible to introduce new stock to some of these groups once they are established. Strangers of both sexes are usually driven out by the dominant residents. In order to introduce new genetic material into the population, it is necessary to do so when new family groups are being established from one to two-year-old animals. New arrivals, with the exception of adult males, are more easily accepted into established chimpanzee and gorilla groups but this has to be carried out in stages, introducing the newcomer to one or two of the residents at a time. There is often a great deal of hierarchical "sorting out" on these occasions and so the process must be carefully supervised.

Primates require a great deal of space and sensory stimulation in captivity. If they are restricted they very often become bored and resort at best to demolishing the cage and at worst to habitual hair plucking or other self destructive vices. Primates will use every available part of their space at all levels and facilities should be provided so that they can use it to a maximum. The larger species, particularly the apes can also be very destructive. Chimpanzees, especially males, will pound doors and panelling, jump continually against the wire mesh and work away at undoing nuts and bolts or weak welded points. Gorillas tend to be more subtle, exploiting any point, such as a loose piece of wire that can be further weakened by regular manipulation. The fabric of primate cages must therefore be frequently inspected and well maintained.

Primates are relatively easy to sedate and anaesthetize once they can be brought into a situation where a projectile dart can be used or where they can be hand injected. All primate exhibits should be constructed in such a way that individuals can be isolated and preferably run into detachable travelling cages or boxes. The best facilities have a movable wall in these small catch up areas so that the animal can be restricted even further and quickly injected manually. At the very least the manager of any primate facility should be able to move his animals into a restricted space without

any "furniture" where the smaller species can be caught in a net and the larger species darted.

Pottos and galagos can be caught by hand or netted with relative ease. Primates weighing between 2 and 10 kg present much more of a problem because although an experienced operator may be able to catch them in a net, they are generally too large and lively for this method. For this size of animal a catch-up cage must be built into the house. Monkeys of at least 5 kg body weight can be darted using a blowpipe and small plastic darts with a 1.5–2.0 cm needle, provided one can get near enough to them.

There are two commercial designs of blowpipe available in Europe, the "Telinject" and the "Distinject". Both are accurate up to 5 m with a little practice but the Telinject, with its better machining, is slightly more accurate over greater distances. This is usually an academic point as one rarely uses such equipment at a greater range. The advantage of the Distinject is that both the pipe and the darts are much cheaper to buy. Both makes of darts have a 2 ml-capacity and the drug is injected by pressure behind the plunger on contact with the animal. When the needle penetrates the animal a polythene cylinder placed over the aperture on the side of the needle is pushed down the needle shaft. This releases the gas or air under pressure which has previously been injected behind the plunger. The metal syringes made by Palmer, Conservator or Distinject are generally too heavy for all but the largest primates, and even then the blowpipe is far preferable providing the target remains at close range. This is because the impact of the syringe and the force of injection is minimal.

The blowpipe equipment has two practical disadvantages for large primates. One is that the pipe itself is impossible to hide and therefore the animals, having experienced it once, realize what is about to happen when it is used again. This can however be an advantage when animals are reluctant to move from one cage to another. The sight of the blowpipe or even something similar is enough to encourage movement in the right direction. The second disadvantage, especially with chimpanzees is that the velocity of the dart is so low that an "experienced" animal can often deflect the projectile in flight. Both these problems can usually be overcome with a little patience and ingenuity.

The drug of choice for use in primates is ketamine hydrochloride (Vetalar—Warner-Lambert) either alone or in combination with a small quantity of xylazine hydrochloride (Rompun-Bayer Ltd). Until recently phencyclidine, an older chemical relative of ketamine, was commercially available, but its manufacture has been suspended because it became a drug of abuse in the United States. Many primate collections still have small quantities of phencyclidine available which they keep for use on the larger species. This is because phencyclidine is much the most potent of the two. Even the largest gorilla would be heavily sedated with 200 mgm of phencyclidine (dose rate 1 mg/kg body weight) which even at its standard concentration (100 mg/ml) only occupies 2 ml.

Ketamine can be bought as the dry powder and dissolved in warm sterile water to give a concentration of 200 mg/ml. Even at this concentration a blowpipe dart will only carry enough of the drug to sedate a 50 kg animal. By reducing the dose rate to 4–5 mg/kg and adding 0.5 mg/kg of xylazine

an animal of nearly twice this body weight can be handled. The combination has the added advantage of producing a greater degree of relaxation and less salivation but recovery may take longer. Surgical anaesthesia can be achieved by using slightly higher dose rates of this mixture and giving further half doses intravenously at 15—20 min intervals as required, or by using additional short acting barbiturates. Sodium thiopentone given intravenously at a dose rate of 2—3 mg/kg after premedication with the ketamine/xylazine mixture is usually used for this. The most practical veins to use are the branches of the superficial brachial on the forearm and the medial femoral. Care must be taken with the latter to avoid the concurrent artery which is usually palpable.

Endotracheal intubation of primates is not difficult in most African species but some of them, notably older apes, have a very soft fleshy tongue and pharynx which tends to obscure the opening of the epiglottis. Other species have a very long epiglottic cartilage and a few have an epiglottis the opening of which is almost at right angles to the line of approach from the mouth and pharynx. Good lighting, usually in the form of a fibre optic cable and telescope, are almost essential for this procedure. Anaesthesia can then be maintained on a closed circuit system with halothane and oxygen in the usual way.

Hyracoidea (Vol. I, pp. 328—351)

All the remarks regarding captive management of rodents are generally applicable to hyraxes.

Pholidota and Tubulidentata (Vol. I, pp. 352—387)

The pangolins and the aardvaark have been placed together as they have many features in common with regard to their biology and maintenance in captivity. Pangolins are rarely seen in zoos but the aardvaark is regularly kept successfully and providing the species can be exhibited in facilities where “day” and “night” are reversed and where plenty of room is available with a large area of sand, or soil to dig in, they are usually very attractive and interesting to the visitor. They have now been bred on a number of occasions in captivity but do not seem in general to be good mothers in this situation. Handrearing the young does not seem to present any real difficulties. Aardvaarks have powerful limbs and can do considerable damage to their enclosures by scratching, pulling and digging unless suitably strong materials are used for its construction initially. Plate glass or perspex windows become scratched very quickly if they can be reached. The species of both Orders feed on ants or termites (see Vol. I, pp. 361, 366, 372, 380). In captivity a similar diet to that given to the Insectivora is usually provided. This consists of minced beef, canned dog food, milk, hardboiled egg and occasionally cheese with added vitamins and minerals. Dog foods, if they are from a reputable manufacturer are usually adequately supplemented

with minerals and vitamins, but meat and egg need added calcium, phosphorus and fat soluble vitamins. There is some evidence from pathological findings in large anteating mammals that they have a high requirement for vitamin K. This is manifest by signs suggestive of delayed blood clotting such as extensive subcutaneous haemorrhages and acute nasal epistaxis. Daily, 100—200 international units of vitamin K, is added to the diet of adult aardvaarks. Nobody accurately knows the vitamin and mineral requirements of insectivorous mammals. In the absence of more specific information a reasonable rule-of-thumb guide to supplementation of an aardvaark diet would be to give 300 iu of vitamin A, 50 iu of vitamin D₃, 3 iu of vitamin E and 2 iu of vitamin K, per kg of body weight. It is probable that the animal can manufacture B vitamins itself and in any case the types of diet fed in captivity are likely to contain adequate levels of most of the water soluble vitamins and of trace elements.

These species are not easy to handle. Both pangolins and the aardvaark are probably best caught physically and then hand injected with a sedative or anaesthetic if this is required. Pangolins can be caught by hand but it is advisable to use gloves as the body scales and the powerful front limbs can inflict cuts. The giant species should be handled with caution (see Vol. I, p. 363). Aardvaarks are almost impossible to hold manually and are probably best held by running them into a net or throwing a net over them and rolling them up in it.

Hand injection can then be carried out into the shoulder or biceps femoris area of the hind leg. Ketamine hydrochloride at a dose rate of 15—20 mg/kg given intramuscularly produces a state of light dissociative anaesthesia in from 8—15 min. The dose rate can be doubled without ill-effects if a longer and more profound effect is needed. The degree of muscular relaxation is likely to be poor, but analgesia is fairly marked. Endotracheal intubation is likely to be almost impossible and so anaesthesia would be maintained on injectable agents alone. Blood samples in the aardvaark can be obtained from the ventral caudal vein or from the larger auricular vessels in the base of the ear.

Sirenia (Vol. I, pp. 388—399)

Because of the difficulty and expense of feeding *Dugong* species, very few have been kept in captivity with any success. They require similar housing facilities to other tropical marine mammals, that is large heated pools with efficient water filtration and disinfection.

The principal difficulty has been to encourage newly caught animals to accept anything other than the marine angiosperms that they feed on in the wild (see Vol. I, p. 394). Anybody contemplating an exhibit of this species must be prepared to take a considerable amount of trouble and to have an open ended budget. The animals will have to be acclimatized to captivity near their point of capture and initially fed on familiar plants. Animals which do not acclimatize to captivity within three weeks should be returned to the sea immediately. Once an animal has become accustomed

to the close presence of humans and is feeding readily, new vegetable foods can be introduced gradually. One zoo found that only lettuce was taken in any quantity, but it is probable that with patience a greater variety of foods would be eaten in time. Although the dugong is probably able to obtain sufficient protein through microbial fermentation in the gut, it is likely that a supplement of trace elements and fat soluble vitamins will be needed especially if the quality and variety of the foods being provided is limited.

There is no published record of sedation or anaesthesia in the Sirenia. A dugong is relatively easy to catch in a net from a small pool and could probably be examined without any physical restraint. Surface manipulations and surgery could probably be carried out using injectable local analgesics only.

If sedation should become necessary, the best procedure for this species, based on its evolutionary connections and the relative safety of the various drugs, would be to try ketamine first (10 mg/kg) then if this did not work xylazine (0.2—0.5 mg/kg) and finally etorphine hydrochloride (1—2 mg total dose). It would be most unusual if one or more of these drugs did not produce a reasonable effect.

Insectivora (Vol. IIA pp. 1—109)

This Order includes the following families:

Potamogalidae	tenrecs and otter shrews
Chrysochloridae	golden mole
Erinacidae	hedgehogs
Macroscelididae	elephant shrews
Soricidae	shrews

Many of the species represented in this Order are not easy to keep in captivity and because they are small and in many cases nocturnal they are infrequently exhibited. A few species of shrew, the hedgehogs and the tenrecs are occasionally kept, the last two families more successfully than the first.

Some details of the diet can generally be found in the individual profiles of species but depending on the habitat in which they are found, all eat a variety of invertebrates and a few will also take small vertebrates including fish, amphibia, birds and mammals. If the opportunity arises, some will eat carrion.

Although it is moderately practical to feed locusts, mealworms and earthworms in captivity, the larger collections would only use these as a supplement to a more artificial diet. Most of the easily available sources of animal protein have been used as a basis in the construction of these alternatives. Usually, a mixture of finely minced beef with chopped hard-boiled egg, and grated cheese, supplemented with in particular, calcium, phosphorus and the fat soluble vitamins A, D and E, is used as a basis. Live cultured invertebrates are then provided occasionally to give variety and to induce more activity. The palatability of the food mixtures may sometimes give rise to problems and a number of other items which can

be tried are the various milk, cheese and meat based baby foods, either as dried powders for reconstitution or in tins. Dog and cat foods based on meat are also often acceptable providing they come from a reputable manufacturer who has balanced the diet with vitamins and minerals.

Many zoos have their own "formulae" which they sometimes claim to be the reason why they do well with a particular species. This may well be the case, but such diets should be carefully examined from a strictly nutritional viewpoint as they are usually only a "variation on a theme" and are often more complicated in terms of the sources of nutrients required than is necessary. The relatively simple digestive tracts of insectivores have a limited capacity for breaking down food items for absorption and metabolic use. For this reason, the main principles to work on are that the diet must be of a high biological value, which effectively means animal protein, and that the main source of energy should be fat with some simple carbohydrates. Most insectivores would be unable to cope efficiently with complex carbohydrates.

Members of the Insectivora are not very sociable and may even be openly aggressive to strange members of the same species. Surface injuries which become infected are one of the most frequent causes of death in this group and this must be born in mind when designing exhibits for them. Sometimes, overcrowding in a cage will cause sufficient stress to increase the animals' susceptibility to disease. This is dealt with in more detail in the section on rodents and the comments made there are in general applicable to most of the smaller mammal species in captivity.

The larger members of the Insectivora are relatively easy to handle and show no undue stress when picked up. Hedgehogs, because of their spines, need to be held with thick gloves. The smaller members of the Order are very difficult to handle for examination and become stressed more easily. They also bite readily. Small hand nets are sometimes useful to catch them if they cannot be trapped in a nest box.

By far the best technique of restraint, both for the animal and the handler, is to use a small perspex box with sliding doors at both ends. Such a box is relatively easy to construct and different sizes from 20 cm to 40 cm in length can be made to accommodate different species according to their bulk. The animal can either be driven into the box, transferred from a nest box, or where feasible enticed into it with food. A 4% mixture of the volatile anaesthetic nallothane (Fluothane—ICI, Nallothane—May & Baker) in oxygen is then pumped into the box through a small (1 cm) hole in its top. Alternatively, halothane can be sprinkled onto cotton wool (2—4 ml for these sizes of box) and pushed through one of the sliding doors. Ether and chloroform, which are still used in some zoos, are no longer acceptable for safety reasons and are in any case less effective and less controllable. Ether is also inflammable.

The animal (never more than one) in the box should be watched closely until it shows signs of lethargy and sleepiness. The box is then tipped gently from side to side until the animal rolls over, becomes relaxed and is unable to right itself. At this point it should be removed from the box. Usually about 3—5 min of light anaesthesia results and can be maintained either by temporary replacement into the box or by using a small face cone with

the pad of cotton wool and halothane in the apex of the cone. Cones can easily be made out of light cardboard or plastic. A technique such as this requires a little practice to perfect. Small mammals lose their body heat rapidly and must therefore be kept warm during recovery which may take up to 1 hour.

Of the injectable anaesthetics available, only ketamine hydrochloride (Vetalar—Warner Lambert) is moderately effective in this group. Intramuscular injections are possible in the smaller species but, to reduce the risk of injury, must be carried out with great care into the muscles of the hind legs. It is more practical and safe to use such an injectable agent in species over 30 g in weight, partly because of the soft tissue damage that may result in an animal as small as some of the shrews and partly because it is difficult to measure an accurate dose of the drug into a syringe when dealing with these minute quantities. The dose rates required to produce moderate sedation range from 2–4 mg of ketamine per 100 g of body weight, the smaller animals receiving the relatively higher rate. It is almost impossible to abolish all movement and obtain satisfactory relaxation with ketamine in these species, and for this reason the first method of anaesthesia is probably to be preferred. A combination of the two techniques is also acceptable for the larger species, where injection is more feasible. Full anaesthesia with relaxation is then produced with halothane but this final part of the procedure must be monitored very carefully to prevent overdosage of the drug. The reactions of the animal should be tested frequently and it should not be left lying in an atmosphere of halothane for more than a few seconds.

Chiroptera (Vol. II pp. 110–341)

From a management point of view this Order can be divided into the fruit-eating Megachiroptera and the insectivorous Microchiroptera.

They are expensive animals to exhibit properly, and few zoo directors have much interest in them. The Chiroptera are not well represented in captivity and with a few exceptions they are difficult to keep. Specific dietary needs, environmental requirements and their social organisations are almost unknown. Where they are shown well, they can be spectacular and fascinating to watch, especially where they are kept active by making them move about in their search for food. The fruit and nectar-eating bats are probably the easiest species in all respects to maintain. Better bat exhibits would probably help to remove the “horror picture” image that the public have of them and so improve the conservation status of the many species that are now under threat.

Although bats are capable of transmitting a number of diseases to humans and close contact with the animals or their excreta in, for example, poorly ventilated caves has occasionally led to such transmission taking place, this aspect of their biology is grossly exaggerated. Only the relatively diminutive vampire bats of Central and South America are known to carry rabies.

Of the African bats, the hammer bat, *Hypsignathus*, which is mainly a fruit eater, has been reported occasionally to attack small animals and possibly to take blood or other body fluids. The heart-nosed bat, *Cardioderma*, is also known to kill vertebrates (Vol. IIA pp. 170—231).

Although most species of bat are highly gregarious, they are also often intolerant of one another in captivity and tend to have a definite hierarchy in their roosting places. This can present a problem, in particular when young males reach maturity and are attacked by older dominant animals. Sufficient roosting sites and a number of feeding points are therefore essential in the management of these animals.

The nectar-feeding species are likely to be more difficult to feed than those that eat whole fruit. It is quite impractical to try to provide anything close to the natural diet and so a palatable substitute must be designed. The digestive tract of the nectar feeder is very short (and not unlike in some respects that of the blood feeders). Both groups of bats in their wild state are taking a "complete" diet in an easily digestible form and doing very little to it apart from absorbing it for metabolic use. This lack of digestive sophistication must be remembered when designing suitable substitute diets for them in captivity. Many animal managers fail to realize the nutritional implications of a species ability to select its food items in the wild, usually from a much greater variety than is available in captivity. Only the most palatable and nutritious petals, pollens and plant fluids are likely to be selected and these will be relatively rich in an adequate range of amino acids and simple sugars. Providing a diet of fruit juice is not the same thing. The ability of the fruit or nectar eaters to cope with more complex carbohydrates is not known, but one would expect it to be limited. The fruit-eating bats tend to extract the pulp rather than ingest the fibrous stroma of the fruit and so may not be ingesting anything very different to the materials swallowed by their nectar-sucking cousins.

Palatability is not as much of a problem in diet construction as it used to be because a wide variety of flavours and even textures can be produced by specialist nutritional laboratories which are usually attached to the major animal food manufacturing companies. In Britain, B.P. Nutrition Products can provide a wide range of specialized foodstuffs for use in non domestic animal feeding and most developed countries have similar facilities available to them.

For those bats which would more readily lap or suck a fluid food, the most practical diet would be based on a soft tinned baby food incorporating milk products but with a fruit flavour. Convalescent foods based on milk or a balanced mixture of hydrolysed vegetable proteins would also provide a suitable starting point. High fat levels are probably best avoided as such animals are unlikely to be able to cope with them. Nevertheless, some fruits, flower petals, pollen grains and nectars are relatively rich in unsaturated fatty acids and small quantities of a balanced vegetable oil could be added to the replacement diet. Energy is best provided using simple sugars, and vitamins can be provided using human paediatric drops. Milk based foods are likely to contain sufficient calcium and phosphorus, but if these are not used, small quantities of an absorbable mineral supplement will be needed. The author has seen cases of nutritional osteodystrophy in growing

fruit eating bats and so supplementation with minerals and with vitamin D is essential.

Those bats which can cope with whole fruit can be offered whatever fruits are available but this should only make up about 50—60% of the dry matter of the diet. It is still important to ensure that ample high quality protein and the correct additional supplementation is provided along the lines given below. Periodic radiographic examination of young adult bats together with an assessment of their growth rates will give an indication as to whether the diet offered is adequate.

From a nutritional point of view, insectivorous bats are likely to be more difficult to establish in captivity as they do not readily take to eating from a container. Young bats which have been weaned and which can be tamed fairly quickly would be the best “starters” for a potential colony. The animals should be given insects, dead or alive, by hand with forceps to begin with and then accustomed to taking these from containers or trays with the bats enclosed in a relatively small space. Ultimately the insects would be mixed with an “insectivore diet” as described previously and this would in time become the sole or major part of the diet.

It is probable that some bats would never adapt to an artificial diet and might have to be given live insects cultured artificially. This is very time consuming and expensive. Anybody contemplating keeping bats which might fall into this category must consider the problems very carefully before attempting such an exercise. It is important to remember that artificially cultured insects may be deficient in certain nutrients, notably calcium. The insect will be a product of what it eats itself. Fly larvae or mealworms cultured, for example, in offal and wheat bran respectively will contain negligible amounts of calcium and probably have a low vitamin A content. It is therefore sound practice to “dust” the insects sparingly with a suitable balancing supplement (Omnivore—B.P. Nutrition, S.A. 37—Hoechst, Canovel—Beecham, Vionate—Squibb).

Bats are not difficult to handle and many are more robust than they may look. Some appear to be susceptible to rapid dehydration (Vol. IIA p. 221). Most of them will bite if given the chance. In captivity, they rarely fly away from a prospective captor and can either be covered with a small soft towel or net and dislodged into it or grasped with a gloved hand. With competent physical restraint, they are on the whole more easily immobilized for examination than the Insectivora. Detailed examination, minor surgery or the taking of blood and other samples will necessitate using the techniques already described previously for the Insectivora. The bats are generally more resistant to ketamine than most of the other groups and may need a dose rate of up to 5 mg/100 g body weight to induce a moderate degree of sedation. Even then, it may be necessary to give additional halothane which when used on its own is probably the best method of inducing anaesthesia in the small species.

Leporidae (Vol. IIB pp. 343—360)

Hares have a reputation for being difficult to keep in captivity. The most successful attempts have usually been where young animals have been handreared and then kept on as adults.

The lagomorphs are obligate herbivores with a considerably enlarged hind gut. Microbial fermentation of complex polysaccharides takes place mainly in the caecum. Hares in the wild eat a wide variety of small plants and, unlike rabbits, can be a problem to acclimatize to the more limited variety of vegetable foods available in captivity. They eat their faeces, effectively recycling lost nutrients (Vol. IIB p. 346). By far the best way to feed hares in captivity is to allow them access to a good quality pasture with a wide variety of plant species. This is not usually practical and in any case, some degree of dietary supplementation is likely to be necessary when fresh grazing is not available.

Where feasible, it is sound policy to try to get the animal to take a proportion of laboratory rabbit pellets in the diet which are then supplemented with chopped fresh vegetables. These pellets are designed to be fed exclusively but it is unlikely that a hare would eat such a monotonous diet alone for very long. All the daily maintenance needs of a 2 kg Crawshays hare would be provided by 100 g of the pelleted diet. Alternatively, 50 g could be provided and supplemented with green vegetables. There is some evidence that lagomorphs are not efficient at manufacturing some of the B vitamins. It is therefore good practice to add either yeast or a multivitamin and mineral supplement to the diet, particularly if a high proportion of vegetable material is used. Other forms of high energy feed which can be tried instead of pellets are a mixture of crushed oats, flaked maize and wheat bran. Prepared cereal foods such as those used for human babies can also be offered.

Despite the considerable amount of work carried out on handling the domesticated rabbit, many of the drugs used to sedate and anaesthetize other species are not effective in lagomorphs. Even very tame hares are very susceptible to stress and they must be handled with great care. If possible, the accommodation should be arranged so that the animal can be driven gently into a box before being picked up. It is very easy to fracture the cervical vertebrae in hares if they are handled roughly. One hand should be placed around the neck and head and the other either under the abdomen or behind the pelvis depending on whether the animal is to be held horizontally or vertically. Either way, the animal should be held close to the handler's body as this helps to further restrain its movements.

Of all the drugs available, a mixture of fentanyl and fluanisone (Hypnorm—Crown Chemicals) given intramuscularly is probably the most effective at a dose rate of 0.5 ml/kg body weight. Nalorpine is used as the antidote. The safety margin is not high and a 50% overdosage may cause respiratory depression.

As with most immobilizing agents, it is best to avoid using them in old animals or those with chronic liver or renal damage. If such animals have to be handled use only 50—70% of the normal dose rates.

Rodentia (Vol. IIB pp. 363—704)

This group consists of the squirrels (pp. 369—443), flying-squirrels (pp. 444—464) the spring-hare (pp. 465—473), mole rats and blesmols (pp. 474—500), myomorph rodents such as gerbils, rats and dormice (pp. 501—676) and the histricomorph porcupines and cane rats (pp. 677—704).

Rodents are not frequently displayed in collections of captive mammals and only the world's largest zoos and a few specialist institutions maintain a comprehensive collection of small mammals. Nevertheless, many of these species have been kept in captivity for various reasons, often by private individuals or research scientists, and in general they are not a difficult group to maintain. Rodent research is of substantial economic importance and properly displayed, the more gregarious rodents in particular make fascinating exhibits. Although most of them need relatively little space they can be very demanding on the materials used for caging. Many species spend a great deal of time in the wild using their incisor teeth to obtain and handle food. A replacement for this activity must be provided in captivity, where food is likely to be readily available and often relatively soft. Adequate supplies of branches, hay and hard coated seeds will usually prevent them turning their attentions to the construction materials of the cage which should in any case be of steel, brick, concrete or at worst, very tough plastics. Larger rodents such as porcupines will even damage some of these materials if they have little else to do.

Quite apart from those species which might be expected to spend most of their lives below ground, many of the larger species, notably the porcupines, will also burrow more extensively in captivity than they do in the wild. Larger rodents are often shown in open exhibits in zoos where the management often forget this fact, only to find that an extensive network of burrows completely undermines the perimeter barrier. Porcupines have been known to dig down over 3 m to get under such a barrier.

Although by far the majority of rodents obtain all their energy requirements from vegetable sources many take animal protein opportunistically. Even apparent specialists like the root rat have been found to include invertebrates in their otherwise vegetarian diet. Rodents are relatively easy to feed in captivity. Once again, it is sound policy to use a commercial cube or pellet designed for laboratory rodents as the basis. This provides some energy and most of the protein and vitamin needs of the animals. Most diets of this type are highly palatable even to rodents that are not used to them. Many animal keepers are averse to using these prepared diets, but often forget that the important aspect for the animal's well being is what nutrients reach the stomach, not what types of food reach the mouth.

Palatability can be improved and activity encouraged by adding, preferably in a second feed of the day if this is practical, a variety of seeds, fruit and vegetables. These might include cereals such as whole maize, wheat, barley, oats and millets, together with sunflower and groundnuts. Chopped carrots, green vegetables, potatoes, apple and roots (turnips, swedes) are also usually provided. The actual constituents might vary

slightly from one group of animals to another based on individual experience. It should be remembered that all these items are deficient in one or more major nutrients, hence the importance of the cubes which should always make up about 50% of the dry weight of the diet. If this proves to be impossible, a high protein supplement such as cheese, milk based convalescent and baby foods or even mincemeat, must be given. Additional fat soluble vitamins (A, D and E especially) will only be necessary if the majority of the diet is limited to cereals and other seeds, especially if, as is likely, they have been stored for some time. High quality seeds which are relatively fresh and have been well cleaned are getting more difficult to obtain for animal feeding, and this is another reason for using commercial diets to a significant extent, where quality control of the product by the manufacturer is a necessity if he is to stay in business.

Rodents, with primates, constitute the greatest risk of any group of transmitting disease to man. Small rodents are known to be involved in the epidemiology of a number of important viral zoonoses, particularly in Africa (Ebola virus, Lassa fever) and probably act in these cases as symptomless carriers of the agent. This should not frighten the prospective keeper providing he takes reasonable precautions. Regardless of the state legislature, all newly imported rodents, especially if they are wild caught, should be placed in quarantine for a minimum of three months. Many countries demand longer periods of isolation. Britain, for example, lists all rodents as potential carriers of the rabies virus and insists on six months strict quarantine.

An established colony is much less likely to be a significant disease risk. Lymphocytic choriomeningitis, for example, has been recorded in colonies of small rodents after many years in captivity, and *Pasteurella multocida* is sometimes the cause of an epidemic, usually manifest by pneumonia and septicaemia, especially if the animals are overcrowded.

Rodents breed well in captivity, but their numbers should not be allowed to build up excessively as the resultant stress very often leads to fighting and other secondary problems such as an outbreak of infectious disease. Overcrowding is also a predisposing factor in the other major management problem of colonial rodents, that of ectoparasitism. Infestations with Sarcoptid or Demodex mange mites are relatively frequent, but a more considerable problem in recent years has arisen, especially in heated exhibits, with *Ornithonyssus bacoti* an opportunistic mite, normally imported with peat or bedding. Once it gains a foothold it is very difficult to eliminate and can live both parasitically on the rodents or as a saprophyte in the bedding.

Bite wounds inflicted by rodents, like those from carnivores, often become septic. Staff should not be placed in a situation where they are expected to handle rodents without adequate training and protection. Catching up facilities can easily be built into most exhibits usually in the form of a removable nest box or trap into which the animals can be fed when necessary. Very small rodents such as the voles and mice can often be enticed into translucent tubes with food in them if these tubes are regularly placed in the exhibit. One end can be blocked with a rubber stopper when the animal has to be caught, otherwise both ends are left open. Live

traps (such as the "Longworth") are also often used. A deft operator can also usually catch animals with a small net such as those designed for use with aquarium fish.

The squirrels and flying squirrels together with other medium to large species are best caught by ensuring that their nest boxes have sliding doors and are removable. Providing such boxes are not continually disturbed, and this is most important, animals will always run back to them as a place of refuge. This arrangement makes the management of such animals much easier.

Species such as the spring hare, cane rats and crested rats often become very tame in captivity and can usually be gently driven in a transport box or caught and held with gloves. To some extent, each operator has to work out the best method of capture to suit his own particular facilities. Porcupines naturally present special problems. Experienced handlers can usually move them into a transport crate with long handled brooms, but these animals are much faster than one might imagine, and will reverse rapidly, spines erect, towards an antagonist if cornered. One of the best ways of catching porcupines is with a large plastic dustbin and its lid. With a dustbin inverted over the animal it can be moved about safely to a corner where the container can be turned on its side and the animal pushed into it with the lid. Porcupines can also be rolled up in a net, and this is often the only way of immobilizing them for injection, although they tend to shed spines liberally if this is done because the degree of handling is inevitably rougher.

Rodents can be immobilized with ketamine hydrochloride but most are relatively insensitive to it and the resultant dose rates needed tend to be high. For the larger species 20–25 mg/kg injected intramuscularly (usually in the main flexor muscle mass of the upper hind leg) produces a moderate degree of sedation with some analgesia, but usually poor relaxation. Smaller species may need up to 50 mg/kg to achieve the same effect.

Rodents up to 500 g in body weight are probably most effectively anaesthetized by subjecting them directly to a halothane/oxygen mixture in the way previously described for other small mammals. A concentration of 4–5% halothane will be necessary for induction, but 2–3% will usually suffice for maintenance and can be given through a mask. Rodents do not seem to find this method stressful and usually sit quietly in a corner of the box unless disturbed. Mild eye irritation is often observed and the animals may blink a great deal or close their eyes in the early stages of induction.

Larger rodents may be sedated with ketamine and the effect deepened with halothane/oxygen given through a mask. Giving intravenous barbiturates to deepen anaesthesia is not really practical in this Order as superficial veins are usually difficult to find. If small quantities of blood are needed, the jugular veins and the medial femoral veins in the inguinal region are the only real possibilities for a sample. Cardiac puncture is not to be recommended unless animals are to be anaesthetised and then destroyed. Blood smears can be obtained by clipping a toenail and gently squeezing a drop of blood onto a slide. Such a minor injury heals readily.

Of all the mammals found in East Africa the carnivores are probably the easiest group to keep in captivity. Many of them live to a considerable age and in the pathology records of the Zoological Society of London one of the most frequent conclusions is "multiple degenerative changes associated with senility".

Despite this many of the smaller carnivores do not breed well or rear their young efficiently in captivity. This is probably due to environmental factors which in many collections are now being corrected. Many carnivores especially the smaller species are nocturnal and, except in specially constructed facilities where the lighting patterns can be controlled, they make poor public exhibits. Carnivores are not as demanding of the fabric of their cages as many other species and, contrary to popular opinion, do not spend a lot of their time trying to tear their enclosures down. Nevertheless, for public safety, the larger species have to be housed using strong materials in case a particular individual is incited to attack its perimeter barrier. In addition, many species are powerful jumpers and climbers, and some of the smaller members of the Order are capable of escaping through very small holes or gaps. All this means that a considerable amount of thought must go into carnivore exhibits not only to make them safe but to make them interesting. In common with the primates, this group is probably the worst exhibited of all zoo animals, especially in some of the smaller collections where they are so commonly kept in aesthetically uninteresting and cramped conditions.

In general, the canids, felids and hyaenids breed fairly well in captivity. Species such as the cape hunting dog and the hyaenas often fail to rear their young successfully and this is probably due in most cases to inadequate cubbing areas, incorrect grouping of the adults such that there is interference from other animals, and disturbance by the staff or the public. These species maintain a very complex relationship within the adult group and between adults and the young, which, if it goes wrong, usually means that the young are abandoned. Now that these factors are more clearly understood, the success rates are increasing. Similar attentions to detail for some of the mustelids and viverrids will probably lead to further successes. Genets and civets for example are often not kept in sufficient numbers to form one or more compatible young pairs. These normally solitary animals are then often kept in too small a space with no room to get away from one another and without suitable facilities for the female to hide and rear her young.

Of the larger East African cats, only the cheetah has been difficult to breed in captivity. A few zoos, notably Whipsnade, have done consistently well with this species, but their secret is still not really understood. One factor seems to be that the breeding animals should not be put together for long periods of time. Female cheetahs rarely show overt oestrous, but hormonal and photolaparoscopic studies show that they do cycle (14—16 days) without the presence of the male. It is probable that when the male is introduced to the female the cyclical changes intensify and mating may

then occur. Males should not be left with the females for longer than two to three weeks at a time.

One of the reasons that carnivores do well in captivity is undoubtedly the ease with which they can be adequately fed. It is as well to remember that carnivorous mammals eat whole carcasses, not just meat. If meat alone is fed, it has to be supplemented correctly to balance the diet. The natural diets of most species found in East Africa are described in some detail in the profiles of species.

Many of the smaller species readily accept the tinned carnivore diets prepared commercially for the pet trade. Providing a reputable manufacturer is used, these foods will have been balanced with added minerals and vitamins. It is unusual, however, for these diets to be taken as the sole source of food and it is usually necessary to provide a small proportion of fresh meat (suitably supplemented) or even whole carcasses in the form of day old chicks, laboratory rodents, rabbits or fish. The more omnivorous species will also take a proportion of cereal in the diet (usually given as dog biscuits) or will accept one of the commercial "expanded" dog pellets. Fruit and vegetables are also often taken in small quantity, although a few species, notably the Palm civet, may take more vegetable than animal foods.

Red meat contains about 20 times as much phosphorus as calcium. Nevertheless, the actual quantity of phosphorus in meat is still relatively small. In order to arrive at approximately a 1·2 to 1 ratio of calcium to phosphorus in the diet, considerably more calcium must be given in the supplement than phosphorus. When the ratio is correct the quantity of vitamin D required is reduced. Most captive carnivores will obtain enough vitamin D from sunlight, but usually the vitamin is added to the diet at a rate of about 1000 iu per kg of meat. Cats, in particular have a high requirement for vitamin A which is not present in meat. This is usually added at a rate of 10,000 iu per kg. Trace levels of iodine are also included. It is not known to what extent, if any, carnivores require supplementary B vitamins or additional vitamin E. Most supplements prepared for carnivores contain low levels of B₁, B₂, B₆ and E. In Britain, a wide range of special supplements and complete diets can be obtained commercially following over 10 years of collaborative research and field trials conducted by the Zoological Society of London and the manufacturer, B.P. Nutrition products.

Most collections feed beef but for economic reasons many also use horse and donkey meat. Some carnivores, cats in particular, will not accept equine meat readily. Calves, sheep, goats, rabbits and poultry are also often used as whole carcasses. With the cats in particular, there is a small risk of bone fragments from these smaller species causing oesophageal obstruction. Poor quality meat can be a source of considerable clinical problems. There are many reports of outbreaks of salmonellosis in carnivores, especially after feeding them calves and poultry. Other pathogenic gut bacteria may also cause problems if the meat has not been correctly stored. Meat from a knackers yard, where the cause of death of the animal to be fed is often uncertain, constitutes a considerable potential risk. Even cases of anthrax and botulism are not unknown after feeding carnivores from such a source. Barbiturate poisoning is another potential hazard when animals have been

destroyed with these drugs and where this fact is not reported to the purchaser of the carcase.

Preferably all the meat purchased, whether it is bought on the carcase or chopped up in boxes, should have been officially passed for human consumption and stamped accordingly. Today this is often not practical nor economic. Meat trading, particularly in lower grade products, has always been an area of business where sharp practice is common and the buyer must be careful to ensure as far as possible that he at least takes meat from animals where their immediate history prior to death was known. The meat inspection service and the local veterinary practice should be asked for advice where necessary.

The principles applying to the physical handling of carnivores have already been described for other groups. The facilities needed will vary from removable nest boxes and trap cages for the smaller species, to built-in crush cages for the large cats, usually incorporated into a passageway that they regularly use. Animals over 5 kg in body weight that can be brought into close range can be darted using a blowpipe. Heavier darting equipment can be employed on the larger species if necessary. A brief discussion of the heavier equipment will be given in the section on ungulates. It is always preferable to be able to hand inject a carnivore using brief physical restraint than to use darts. This is mainly because hand injection can be carried out accurately and with more certainty. Ketamine alone, or a mixture of ketamine and xylazine, is preferred for most of these species. In general, the smaller carnivores are less sensitive to the cyclohexamines than the larger ones and may need up to 30 mg/kg of ketamine intramuscularly to achieve a useful effect. The cats are the most sensitive (8–12 mg/kg). The canids and hyaenas come between these two levels at about 15 mg/kg. Because ketamine is not particularly potent, relatively large volumes of the drug may have to be injected and this is often not practical. By combining ketamine with xylazine, the drugs potentiate each other and so reduce the doses of each which would have to be used if they were acting independently. In cats, a state of light anaesthesia can usually be obtained with 5 mg/kg of ketamine and 0.5 mg/kg of xylazine. This mixture has not been tried in the other African carnivore families, but it would almost certainly be worth doing so when an opportunity arises, at slightly higher dose rates than those above.

Xylazine alone has also been used in many of these species but the dose rates required are usually very high and therefore expensive. Etorphine hydrochloride is also reasonably effective in the canids and hyaenas but relaxation is usually poor, salivation is often profuse and the safety margin is much less than for the other drugs.

The jugular vein is usually the easiest vessel to obtain blood from in these species although none of the superficial vessels are obvious in many of the smaller carnivores. The alternative vessels for the larger species are the brachial on the anterior forearm and the recurrent tarsal vein just above the hock. For the smaller species, only the medial femoral vein in the inguinal region is usually practical. Surgical anaesthesia can be achieved with higher doses of the ketamine-xylazine mixture. Another alternative is to use additional sodium thiopentone at 3–4 mg/kg body weight which must be

given intravenously. Intubation and maintenance of anaesthesia on halothane and oxygen then follow.

Proboscidea

Much of what will be discussed about the management of ungulates is applicable to the African elephant. Needless to say, accommodation for such a large mammal must be extremely tough and durable, not only because of the animal's considerable strength and weight but because elephants will "test" the fabric of their enclosures in a way which no other large herbivore will try. Any object or fitting which can be gripped in the trunk, pushed with the forehead or have weight applied to it will be subjected to this trial. In addition the enormous output of faeces and urine creates a special cleaning problem, especially as this species is one of very few that will actively distribute its dung into areas well outside the normal confines of its enclosure.

The elephant, like the equids, digests cellulose in its large intestine. It is both a browser and grazer and can be fed successfully in captivity using either horse or cattle cubes. Most collections try to give elephants a varied diet with both lucerne and meadow hays, cubes or loose cereals with protein and vitamin supplements and vegetables. Branches, even with tough bark are usually relished not only for their nutritional value but also as occupational therapy and for working worn teeth loose. The teeth are replaced regularly and dental problems leading to inappetance will often result if elephants are not given branches to chew. Elephants like horses are very subject to minor digestive disturbances. Both diarrhoea and constipation are relatively frequent occurrences if the diet is not consistently of a good quality. Public feeding, and the ingestion of foreign bodies and dirty water are also common causes of these problems.

Young elephants, especially between one and five years of age are prone to nutritional bone disease which is often caused by an excess of calcium in the lucerne hay with very little phosphorus in the rest of the diet to balance it. The situation is often made worse where young elephants are denied access to natural sunlight for much of the year. The solution is to feed a mixture of hays, some wheat bran for its phosphorus content and to add a comprehensive mineral and vitamin supplement to the diet.

Once a young elephant has been acclimatized and is feeding well, they generally have very few problems. *Grammocephalus nematodes* in the bile duct can cause obstructive jaundice in new arrivals and the eggs of this parasite should be looked for in the faeces. Skin and foot care is essential in this species from an early age and regular bathing and scrubbing in warm water is recommended.

A number of drugs are capable of producing sedation or narcosis in elephants. Xylazine is the drug of choice for sedation and etorphine with acepromazine for full immobilization and analgesia. Dose rates are given in the table. Intubation is surprisingly easy in the African elephant but other than acting as a method of maintaining a patent airway the technique

is of little value for closed circuit anaesthesia because reservoir bags have not yet been made to accommodate the tidal volume of all but the youngest of this species.

Ungulates i.e. Perissodactyla and Artiodactyla (Vols IIIB, C, D)

These very diverse and numerous herbivorous animals can be discussed together because they present similar management problems. Because the ungulates are so diverse and spectacular, many of them are regularly displayed in zoos. In general they are not too difficult to keep; most of them adapt readily to temperate climates but good housing and yards, are essential in northern winters. Despite the fact that many African ungulates are highly gregarious in the wild, the same species, blue wildebeeste and common zebra for example, can often be very intolerant of other members of the group in captivity even when they are given plenty of space. Although some species can be housed together in small numbers, others, such as sable and roan antelopes, should ideally be given separate loose boxes at night in colder climates. This applies especially to adult males and females with young at foot. Many owners dislike the idea, but the fact remains that the best results are usually achieved when the animals become used to close handling by humans and can be managed as if they were domestic stock. This becomes especially useful when stock have to be separated for feeding, to give birth or for immobilization and examination.

Good ungulate exhibits are expensive to build and as these species are also costly both to import through quarantine and to feed and staff, considerable thought must go into planning them. A number of basic features are common to the construction of all exhibits for these species. It is essential that an early decision is made on the maximum number of adults to be held. The housing complex should consist of adequate hard surfaced yards and loose boxes to accommodate the adults and up to two successive births of young animals. The housing should take account of keeping spare adult males for breeding purposes and older juveniles which have not been accepted by the herd. Loose boxes will be needed in many cases for females to have their young in relative isolation and the same boxes may also be needed at other times to isolate minor cases of injury or sickness. Sliding doors which do not jam easily and which have no projections should be fitted between each box. The construction of the barriers of these areas should be such that animals cannot get entangled or otherwise damage themselves in or on them and that they cannot fight with other animals through or over the barrier. Even some relatively small species are capable of jumping 2 m and eland and roan will go over 2.5 m if there is an incentive to do so. Some of the larger antelopes and the Cape buffalo will often attack wire netting or cables and rip them up, but this is usually a problem with particular individuals, most often males. Many ungulates faced with unfamiliar enclosures where the barriers are not solid may try to run through them severely injuring themselves. This is particularly so if animals are released from dark travelling boxes. Very often

it is worth hanging black hessian sheeting around the enclosure or tying wattle hurdles to the wire temporarily until the occupants have settled down.

Ditches with solid walls are usually the best barrier around ungulate paddocks and are also one of the best ways of the visitor viewing the occupants. Such construction is very expensive and most zoos have to resort to using 12 gauge chain link mesh supported on straining wires running through steel uprights. This will hold all except the pigs and the largest species, buffalo, hippopotamus, rhinoceroses and giraffe. The pigs require a solid barrier at least up to 1 m in height which also extends 0.5 m below ground level, otherwise they will excavate underneath it. Although giraffe can be kept behind wire mesh reinforced with horizontal steel poles and the white rhinoceros will usually stay behind parallel steel cables under high tension, the other large species require a much more solid barrier, either brick and concrete walls or vertical steel poles embedded in firm foundations and reinforced with a horizontal bar 2 m above the ground. A secondary smaller barrier is also usually needed to keep visitors away from the primary barrier. Electric fences as a means of controlling such animals have a very limited application. Only when the wires are placed in parallel rows close to the ground are they effective for a few species such as the white rhino and Arabian camel, but many antelopes become aggravated by these devices and rip them out with their horns.

As with all other species it is essential in the housing design to plan a practical method of capturing individual ungulates with the least possible stress and the lowest risk of injury to themselves. Of all East African mammals, the antelopes in particular are the most prone to accidents during capture and subsequent release. If it is practical to keep animals tame and used to their handlers being close by, such accidents are far easier to avoid. Animals can often become quiet enough to allow hand injection and this is often true of, for example, rhinos. Usually, the larger species have to be darted and the first prerequisite for this is to be able to contain the animal on its own in a relatively small area such as a loose box where it cannot damage itself easily. Even very small species such as dik-dik can be caught using a blowpipe dart providing they can be enticed into a restricted holding area where they are at close range and not panicking. If this is not feasible, the other alternative for small ungulates (gazelles, duikers, dik-dik) is to have a narrow passageway with high, smooth, solid walls built into the house, preferably through which the animals pass every day. From time to time such a passage can be partly filled with soft bedding and the animals caught in it physically by experienced handlers. Hand injection of immobilizing agents can then follow.

For most East African ungulates feeding does not present any major problem although some of the high concentrate feeders or browsing species are more difficult in this respect than the grazers. Inevitably, because of their physiological affinities with larger domestic mammals the design of diets for these species has been based on our knowledge of cattle, horse and pig nutrition. Many commercially available diets are designed for production rather than maintenance and these are best avoided. Even at the height of lactation, a female in good condition can either draw on available reserves for this relatively short period or increase her intake of

the maintenance diet fed to the group throughout the year. Most animal managers will make the necessary temporary adjustments in the diet when it is required.

Maintenance level cubes designed for adult non pregnant sows are adequate for the wild African pigs and can be supplemented with a variety of chopped fruit and vegetables. Pigs given access to grazing will also utilize this but tend to make the exhibit unsightly as they dig the ground up.

The equines should be given low energy, low protein, cubes designed for domestic ponies. These usually contain about 20% fibre and can be fed as the sole source of food. Usually, a good quality meadow hay is used to replace part of the cube intake. Zebras with access to reasonable grazing in the summer months rarely need anything else and will quickly become overweight and probably develop laminitis if the quality of the diet is too high. Zebras in the wild are capable of living on diets of extremely poor nutrient values for long periods of time.

The hippopotamus and those ruminants which are predominantly grazers, such as the alcelaphines and the kobs have little difficulty coping with a diet suitable for beef cattle. This is based on a relatively low energy, low protein cube with meadow hay and in many collections a supplement of root vegetables is given when they are available. The more specialized a ruminant is in terms of its habitat and the food plants it takes from that habitat the more of a problem it becomes to feed adequately in captivity. This is partly due to the fact that it will not eat a relatively monotonous diet consistently and partly that such species seem to be more prone to some dietary deficiencies, notably of the essential fatty acids although the precise definition of many of these problems has still to be elucidated.

Species such as eland, beisa oryx and buffalo which may browse to a considerable degree in some areas are highly adaptable and will take standard cattle diets but most of the tragelephines, the sable antelope, the duikers, the gerenuk and the giraffe require a wider variety of foods including lucerne or clover hays, fresh branches and vegetables. They appear to require somewhat higher levels of protein and probably in captivity often receive inadequate levels of fatty acids and vitamin E. Vitamins can be given as a supplement, but additional unsaturated fatty acids are hydrogenated by the rumen and therefore fail to benefit the animal. In recent years a number of pathological problems in these species including distorted red blood cells, low birthweights and poor neonatal survival, chronic muscle wasting and cardiomyopathies suggest that deficiencies of fatty acids, vitamin E and possibly the trace elements selenium and copper may all be involved. At the present time work is being carried out to try to find a way of stabilizing fatty acids in an artificial diet so that a moderate proportion of them reach the duodenum unchanged. Meanwhile, the only alternative is to feed these species on as wide a variety of foods as possible, some of which are rich in the long chain fatty acids.

Most of the serious problems seen in captive ungulates are either caused by injuries or relate to some disturbance of their digestive system. Infectious disease in established groups of these species is rare. Apart from the management topics discussed briefly above, two other subjects, endoparasitic control and footcare, are important both at the planning stages

of ungulate exhibits and for day to day care. Ungulates not only bring in endoparasitic helminths of their own but are also often susceptible to many further species normally carried by other ungulates, domestic and non-domestic. Efforts should be made to prevent cross-contamination of exhibits, to keep animal stocking densities to a reasonable level, remove as much faecal material as quickly as possible from the enclosures and where necessary conduct a regular worming programme with modern anthelmintics.

The hooves of most ungulates in the wild are kept worn down by continuous movement over relatively abrasive surfaces. In captivity, the hooves of some species, notably giraffes and zebras grow quickly if they are not housed on surfaces where such abrasion can take place. This problem is basically one of planning but even then certain individuals for various reasons continue to grow long hooves and need to be regularly restrained or totally immobilized for attention to their feet.

Apart from the blowpipe darts mentioned earlier, a number of heavier darts are made to carry larger volumes greater distances. The best known of these are the Palmer "Cap Chur" guns (U.S.A.), "Distinfect" (Switzerland), Conservator (U.K.), Daystate (U.K.), Paxarm (New Zealand) and Simmons (U.S.A.). Van Rooyen makes equipment for use in South Africa but this is not available elsewhere. Various "home made" weapons are also in use and further systems are produced in eastern bloc countries for their internal use. Two systems use compressed air or gas to propel the dart but most utilize a blank cartridge. In some cases different grain loads of powder in the cartridge are used to achieve different muzzle velocities, while in others the velocity is altered by an adjustable valve fitted between the cartridge chamber and the dart.

Most of these darts consist of aluminium alloy barrels although those of the Paxarm system are plastic. Some of the darts are composite but the majority are assembled from a barrel, needle, tail piece and plunger. Injection on impact with the animal is produced either by an exploding cartridge or by air or gas pressure initially pumped into the back of the dart assembly. Some needles have an aperture at their tips, others on their sides. The needles can be purchased in varying lengths with or without a cuff or a barb. In general it is always wise to use the longest needle which is practical without causing excessive damage. In thin skinned animals it is also wise to use a needle with a cuff or barb to prevent the dart rebounding before it has injected all the drug.

Most of these weapon systems are now comparable in performance and quality. None are accurate over about 35 m, despite the claims of their manufacturers. In practical tests, darts were fired into a 15 cm square from the clamped weapon. If 10 similar darts fired in succession all fell into the square at a particular distance the weapon was considered to be accurate at that distance.

Although blowpipes are preferable for use in enclosed areas where only small volumes of drug need to be injected, longer range weapons are still usually required in most ungulate collections. Darts must be fired at right angles to the surface of the animal and only the muscle masses of the shoulder, neck and hind leg should be aimed at. Usually only one chance

a day is available to hit an animal successfully under field conditions, so the preparation of the equipment, stalking and assessment of the situation must be careful and accurate.

The table lists the dose rates of various drugs recommended for use in East African ungulates. Although xylazine alone is used extensively in some collections, it has the disadvantage of most sedatives in that the dose rate varies markedly not only from one species to another but also between individuals of the same species where their temperaments may be different. By far the most universally accepted drug for this purpose is etorphine hydrochloride (M99 Reckitt and Colman) which is used in combination either with acepromazine maleate (A.C.P.) or xylazine. An M series morphine antagonist diprenorphine (M. 50—50) is used to reverse the main narcotic effects and is given, at a dose rate 1.5 times higher than that of the original etorphine. Under field conditions the antagonist is usually given intravenously, but if a slower recovery is needed, such as when an animal is introduced to a travelling crate or a strange loose box, it is often preferable to give M.5050 intramuscularly. All wounds caused by the dart needle should be packed with intramammary penicillin after the dart has been carefully removed. It is also wise to give the animal long acting penicillin by intramuscular injection to prevent any secondary infection occurring.

Full surgical anaesthesia is rarely induced in ungulates, especially ruminants, probably because of the limited amount of deep tissue surgery that is practical and the general difficulties of carrying out some of the procedures involved, notably endotracheal intubation. When the occasion demands it, xylazine alone should be used as the premedicat in ruminants, ketamine in pigs and etorphine in rhinos and zebras. Once the animal is recumbent, anaesthesia is usually induced using either sodium methohexitone or sodium thiopentone given intravenously to effect. In ruminants, intubation should always be carried out once the animal is relaxed because of the possibility of regurgitation. In the other species it is desirable but not as essential. Anaesthesia can be maintained either with additional doses of barbiturates or with halothane and oxygen if intubation has been possible.

DOSE RATES AND DRUGS FOR THE IMMOBILIZATION OF LARGE HERBIVORES

Species	Adult weight range (kg)	Etorphine (M.99) Total dose (mg)	Sedative Total Dose (mg)	Comments
Kirks dik-dik	2—3	0.2	1 Xylazine	Blowpipe only
Grey duiker	10—12	0.4	4 Xylazine	Blowpipe only
Thomsons gazelle	16—20	0.6	6 Xylazine	Blowpipe preferably
Bushbuck	30—40	0.8	10—12 Xylazine	3 cm needle
Grants gazelle	45—55	1.0	15—20 Xylazine	3 cm needle
Common reedduck				
Sitatunga	60—80	1.0—1.2	25—35 Xylazine	3 cm needle
Lesser kudu	75—110	1.2—1.5	40—50 Xylazine	4 cm needle
Beisa oryx				

Species	Adult weight range (kg)	Etorphine Total dose	Sedative Total Dose (mg)	Comments
Waterbuck	150—200	1.8—2.2	50—60 Xylazine	5 cm needle
Greater kudu	150—250	1.8—3.0	70—120 Xylazine	5 cm needle
Okapi	170—250	2.0—3.0	70—120 Xylazine	5 cm needle
Roan antelope } Sable antelope }	200—300	2.5—3.5	100—150 Xylazine	6 cm needle
Eland	300—500	3.0—4.5	150—250 Xylazine	6 cm needle
Cape buffalo	500—700	4.0—6.0	200—300 Xylazine	7 cm needle
Topi } Kongoni }	120—160	2.0—2.5	10—12 Acepromazine	5 cm needle
Wildebeeste	150—200	2.0—2.5	10—12 Acepromazine	6 cm needle
Somali wild ass	200—250	2.0—2.5	10—12 Acepromazine	5 cm needle
Common zebra	250—350	2.5—3.0	12—15 Acepromazine	6 cm needle
Giraffe	600—800	4.0—5.5	20—30 Acepromazine	8 cm needle Legs tied quickly. Neck raised. Narcotic reversed as soon as possible. Providing physical support provided.
		— OR —	600—800 Xylazine	
Black rhinoceros	1300—1500	3.0—3.5	12—15 Acepromazine	8 cm needle
White rhinoceros	1700—2000	3.0—3.5	12—18 Acepromazine	8 cm needle
African elephant	3000—5000	5.0—7.0	30—50 Acepromazine	8 cm needle Support needed ideally
		— OR —	500—800 Xylazine	8 cm needle Support needed ideally

Xylazine can be used alone for sedation in all ruminant species. Dose rates will vary from 1—6 mg/kg dependant on species and temperament.

Species	Adult weight range (kg)	Etorphine Total dose	Sedative Total Dose (mg)	Comments
*Warthog	40—70	400—700	40—70	Narcotics (etorphine) have been used but not very safe.
Bushpig	60—110	600—1000	60—100	

* Early trials of 5 mg/kg of ketamine and 0.5 mg/kg of xylazine in pigs suggest that this may ultimately be the mixture of choice.

Appendix III

Disease and Parasites

Diseases are among the major factors controlling animal numbers, including the numbers of humans and their domestic species. Populations can increase or be depleted through the absence or presence of disease and such changes in numbers, particularly in large herbivores, can induce substantial and sometimes long-lasting alterations in vegetation and in the predator and other communities within the habitat.

Diseases are no respecters of boundaries, whether between nations, parks or farmland. Some can threaten all mammal species impartially.

The knowledge that many fatal or damaging diseases can pass from one species to another and in epidemic proportions, invests this complex area of biology with medical, agricultural, economic and political significance. The dangerous consequences of diseases puts a heavy responsibility upon all who attempt to understand and control them. There is therefore a pressing need for close communication between workers in this field and other biologists. The former recognize that diseases and parasites exist within ecological matrices as intricate as those of their hosts. Ecologists recognize the reverberating effects of diseases on habitats and on many other aspects of mammalian biology.

Some mammal populations are known to harbour diseases that affect humans or their livestock. As human settlement has expanded people and livestock have come into more frequent and intimate contact with wild animals. Important communities and sanctuaries for rare species increasingly face destruction because they are seen as reservoirs of disease or refuges for pests.

This is but one of the more immediate reasons why diseases in wildlife must not merely be controlled, they must be studied and understood.

Diseases in man and livestock are controlled by means of compulsory treatment regulations and through extensive public health and veterinary services. The principal means of controlling diseases in wild animals has been to shoot all animals in a *cordon sanitaire* around the areas to be protected. The most extensive of these cordons was initiated in 1913 and has permanently denuded a huge area between Lakes Tanganyika and Lake Nyasa (Malawi) of all large mammals (see distribution maps). This very expensive campaign was designed to control rinder pest under the erroneous belief that wildlife constituted a reservoir. Most African ruminant species die from rinderpest but if they develop immunity they do not continue to be carriers and a non-lethal form of the disease has not had time to develop, rinderpest having been introduced into Africa in the late nineteenth century. Cattle, on the other hand, are reservoirs and have been the source of all outbreaks in wild ruminants. Once cattle were fully protected by vaccination campaigns the disease died out.

It took 80 years for the veterinary profession to correct its assumptions. The main reason for the mistake was low priority for research in wildlife. Fear of disease and the unknown still governs the attitudes of decision-

makers at many levels of government and actions frequently operate to the disadvantage of wildlife. The fear of unknown diseases is justifiable however and there can only be one resolution—to redouble our efforts at understanding them.

A new generation of veterinarians is now questioning the long-held presumption that all forms of wildlife are incompatible with animal husbandry and human progress. The practical problem of managing immensely complex tropical ecosystems (including their diseases) are being approached more realistically by a small cadre of thoughtful Development specialists. Notable among these are veterinarians of the Kenya Wildlife Disease Research Unit.

The alternative, wholesale conversion to controlled and controllable agricultural systems is still the dominant philosophy. This, quite logically, necessitates the destruction of all indigenous fauna and flora.

Some of the indigenous ecosystems that are being destroyed are more productive than the best agricultural lands in Europe, in terms of protein production, biomass and turnover yet the same can seldom be said for the production that replaces it.

Disease is a major obstacle to the development of mixed animal ranching but it is not an insuperable obstacle. The presence of disease and particularly parasites has also been a major inhibitor of the exploitation of wild herbivores for meat because susceptibility of humans and domestic animals to larvae, cysts etc has not been investigated. Disease in wildlife is therefore one of the major constraints on the development of Africa and of its wildlife resources. Vigorous open-minded enquiry into the biology of wildlife diseases is needed with full recognition of serious implications for human development.

This appendix lists some of the better known diseases and parasites. There can be little doubt that many new pathogens await discovery. One of the least understood aspects of disease is the role of complexes; while they are well fed and undisturbed wild animals commonly tolerate heavy parasite loads together with numerous and diverse pathogens but succumb when they come under stress.

Another little-known area is the evolutionary history of diseases and parasites. Is a host-specific pathogen more recently evolved? Is it a specialized lineage that has followed its host's evolutionary course step by step? Are pathogens with a wide host tolerance long established? Does their catholicity have predominantly environmental or evolutionary implications? There are examples of primitive parasites on conservative relic host species while the more advanced and successful mammalian host has more specialized and highly evolved parasites (Vol. IIB p. 546).

I hope that the ecological and evolutionary dimensions of these volumes may suggest lines of enquiry that may lead towards a broader understanding of diseases.

Much important and interesting work has been done but for reasons of space this has had scant recognition in these volumes. Only a brief list with supplementary notes can be offered here. Davis and Anderson (1970—1971), McDiarmid (1968), Round (1968), Page (1975) and various FAO/UNDP reports should be referred to for further information.

Organisms are listed in five categories—viruses, protozoa, bacteria, endoparasites, ectoparasites.

Bacteria and Mycoplasma

Anthrax (Bacillus anthracis). A universally distributed and virulent disease caused by long-lasting bacillae in food, soil or water. Causes swelling of tissues and exudation or tarry blood from orifices. Waterholes may provide ideal incubation conditions. Affects artiodactyls, the elephant, carnivores and occasionally humans and other mammals.

Brucellosis. Contagious infection by *Brucella abortus* and *B. melitensis* which cause swelling, bleeding and abscesses in many organs. Commonly found in cattle, goats, buffalo, eland and zebra. Communicable to humans.

C.C.P. Contagious pleuropneumonia. Caused by *Mycoplasma* species. Affects cattle, sheep, camels and buffalo. Antibody to caprine type (C.C.P.P.) recorded in impala.

Johnes disease caused by *Mycobacterium johnii*, scarce.

Leptospirosis (Leptospira spp.). A widespread disease infecting man and most mammalian species. Of little importance in East Africa.

Plague (Pasteurella pestis). An acute infectious disease multiplying in the gut of fleas (*Xenopsylla*) parasitizing rats (mainly *Rattus rattus* and *Praomys natalensis*). Death from multiple haemorrhagic buboes. In Uganda about 20,000 people died of plague between 1928—1938. Cause of decline of virulence and prevalence not fully understood.

Pseudotuberculosis (Yersinia pseudotuberculosis). An acute lymphangitis causing lesions in the viscera. Can attack most mammal species.

Salmonellosis. (*Salmonella* spp.) carried by *Rattus norvegicus*. Contamination causes severe food poisoning in humans.

Shigella flexneri and *S. sonnei* cause dysentery in primates.

Staphylococcosis (Staphylococcus spp.). Ubiquitous disease affecting artiodactyls, carnivores, rodents and lagomorphs.

T.B. Tuberculosis (Mycobacterium bovis and M. tuberculosis). Chronic infectious disease. Can attack all mammal species and cause severe inflammatory tissue in various organs.

Tularemia (Francisella tularensis). A plague-like infectious septicaemia occurring in Rodents and Lagomorphs. Communicable to man.

Endoparasitic Helminth Diseases

There are three classes of helminths: Nematodes, Cestodes and Trematodes. Helminth disease is commonly manifested in heavy parasite loads of such helminths as tapeworms and lungworms, and in conditions such as Trichinosis.

Common genera of helminths in East African artiodactyls are: *Agriostomum*, *Avitellina*, *Bunostomum*, *Carmyerius*, *Cooperia*, *Cooperoides*, *Cordophilus*, *Cotylophoron*, *Dictyocaulus*, *Echinococcus*, *Fasciola*, *Haemonchus*, *Impalaia*, *Longistrongylus*, *Moniezia*, *Monodontella*, *Oesophagostomum*, *Paracooperia*, *Setaria*, *Stilesia*, *Strongyloides*, *Trichinella*, *Trichostrongylus*.

Perissodactyls are parasitized by *Anoplocephala*, *Crossocephalus*, *Cycliocycylus*, *Cylindropharynx*, *Habronema*, *Kiluluma*, *Oxyuris*, *Setaria*, *Strongylus*, *Trichonema*.

Hyraxes suffer from *Anoplocephala*, *Inermicapsifer*, *Setaria* and *Trichuris*.

Elephants have *Amira*, *Brumptia*, *Bunostomum*, *Grammocephalus*, *Leiperenia*, *Loxodontofilaria*, *Murshidia*, *Pabronema*, *Protofasciola*, *Quilonia*.

Common carnivore helminths are *Ascaris*, *Brugia*, *Cyclicospirura*, *Diphyllobotrium*, *Echinococcus*, *Filaria*, *Mesocetoides*, *Physaloptera*, *Sparganum*, *Taenia*, *Tetrathyridium*, *Trichinella*.

Common primate helminths are *Oesophagostomum*, *Filaria* and *Strongyloides*.

Ectoparasites

Fleas
Lice
Mites

Pentastomes (endoparasitic arthropods) are important parasites of the respiratory tract in some artiodactyls and carnivores.

Ticks are important vectors of infectious disease. Common genera are *Amblyomma*, *Boophilus*, *Haemaphysalis*, *Hyalomma*, *Ixodes* and *Rhipicephalus*. *Boophilus decoloratus* is the main vector for *Babesia* in cattle, *Ornithodoros* for African swine fever, *Rhipicephalus appendiculatus* for N.S.D. The flea *Xenopsylla cheopis* is the vector of plague.

Protozoa

Amoebiasis. (*Entamoeba* spp.). Intestinal infection affecting primates.

Anaplasmosis. (*Anaplasma* spp.). Antibodies prevalent in many wild artiodactyl and perissodactyl species. Infectious disease causing anaemia. Pantropical.

Babesiosis. (*Babesia* spp.). Virulent tick-borne disease of felids, equines, elephant and domestic cattle. Not recorded in wild Bovidae but antibodies prevalent.

B.P.F. *Bovine petchial fever.* Fever especially affecting sheep. Positive isolations of carrier status identified in bushbuck.

E.C.F. *East Coast Fever, Theileriosis.* A virulent tick-borne disease of Artiodactyla in which *Theileria* piroplasms invade erythrocytes. Twelve species described; some host-specific (i.e. *T. taurotragi*, a natural cause of mortality among eland, Grootenhuis 1979). E.C.F. causes annual loss of approximately half a million cattle in East Africa. Buffalo may be reservoir for *T. lawrencei*. Other wildlife species not yet implicated but more research needed. A piroplasm, *Nuttalia loxodontis* has been identified in the elephant.

Malaria caused by *Plasmodium* spp. and *Hepaticystis* affects many primates, rodents and other mammals.

Trypanosomiasis. Disease of the blood system caused by *Trypanosoma*. Vector Tabanid tse-tse flies (See Vol. I p. 108 for distribution). Various species of *Trypanosoma* can affect most mammal species, including man. Prevalence of tse-tse and trypanosomiasis is reason for absence of domestic livestock and low human density in *Miombo* woodland belt (See Vol. I pp. 24, 108). Control methods include destruction of hosts and habitat (i.e. all large mammals and trees) and spraying of insecticides.

Other protozoan diseases *Besnoitiosis, Toxoplasmosis.*

Viruses

A.H.S. *African horse sickness.* Mainly equine disease, prevalent in zebras, may also occur in elephant.

A.S.F. *African swine fever.* Severe infection affecting all African pigs. Tick-borne (mainly *Ornithodoros* spp.) and may be arthropod virus incidentally attacking pigs.

B.T. *Blue tongue.* An infectious catarrhal fever. Arthropod vector. Inflammation of mucous membranes. Affects Artiodactyls and reported from Rodents (*Rhabdomys* and *Otomys*).

- B.V.D. *Bovine virus diarrhoea*. A viral disease attacking Bovids. Recorded from eland, rare.
- DIST *Distemper*. Acute febrile disease of carnivores resembling para-influenza. Known to affect African hyaenids, canids and viverrids.
- E.H.D. *Epizootic haemorrhagic disease*. Acute infectious disease affecting ruminants.
- F.M.D. *Foot and mouth disease*. Virus mainly affecting Bovini, causing lesions in feet and mouth. Buffalo a reservoir. Mechanism of infection imperfectly understood. Buffalo not normally a source of infection for cattle.
- F.P. *Feline Panleukopenia*. Acute viral enteritis in felids, known from lion, leopard and cheetah.
- I.B.R. *Infectious bovine rhinotracheitis*. A viral infection of the respiratory tract, known to affect buffalo and gnu.
- I.C.H. *Infectious canine hepatitis*. Affects mainly dogs.
- M.C.F. *Malignant catarrhal fever*. A prolonged viral infection, inflammation of the respiratory system, eyes and gut. Affects all ruminants but Alcelaphini and Bovini especially.
- Myxomatosis*. Pox virus. Insect vector. Attacks lagomorphs and squirrels. Originates in South America. Not yet recorded from East Africa.
- N.S.D. *Nairobi sheep disease* (probably synonymous with *Granjam virus disease*). A tick-borne virus mainly affecting *Ovis*.
- RAB *Rabies, Rage*. Predominantly a carnivore disease. Acute infection of central nervous system caused by virus in salivary gland. Varied symptoms i.e. "furious rabies" to "dumb rabies". Jackals thought to be main reservoir in Africa.
- R.P. *Rinderpest*. An RNA virus similar to measles and canine distemper. Attacks all artiodactyls with death from dehydration following severe fever, gastroenteritis and diarrhoea. Contagion through direct contact or airborne virus emanating from all discharges. Originated in Eurasia, entered eastern Africa in 1890. Now very sparse in East African countries due to sustained immunization campaigns on cattle.
- R.V.F. *Rift Valley fever*. Viral disease affecting many species. Low prevalence.
- Virus B infection*. Herpes infection, mild in monkeys. May cause fatal encephalitis in humans.

Other viruses affecting mammals: Bahig, Bunyamwera, Burg el Arab, Congo, Chikungunya, ephemeral fever, Hazara, Kadam, Matanya, Nyamaini, Semliki Forest, Sindbis, Tete, Thogoto, Upulu, Uukumeni, West Nile, Yellow Fever, Zika.

Appendix IV

Exploitation

This book concerns a fauna, its basic biology and evolution. The management of mammals as an economic resource is outside the purview of these volumes involving, as it does, several complex and specialized disciplines. Nonetheless some of the information that has been presented should be relevant to those authorities and enterprises that would attempt the responsible and sustainable exploitation of mammals and a few observations may not be out of place. How those that exploit mammals go about it will largely determine the fate of many important species.

The fauna and flora of Africa has been exploited by humans from our earliest beginnings. Most people will catch animals for food if it is not too much effort and most will trade in bits and pieces of animal if there are sufficient inducements. Animals continue to be exploited on a large scale in East Africa because they are numerous, widespread and varied. It is nonetheless broadly true to say that most of this exploitation can find no recognition in economic analyses or balance-sheets because most of it is submerged, unrecorded, unquantified and currently unquantifiable.

This is not only true for elephants and rhinos (see Volume IIIB, pp. 66—75; 103; 118 and Parker's 1979 report on the ivory trade) but applies equally to animals killed for meat. Trading in wild animal meat is illegal. At an early date the interests of a budding livestock industry coincided with the views of colonial game wardens to place a fairly effective embargo on open trading in wild meat. Nonetheless throughout East Africa hunting contributes to the nutrition, variety of foods, recreation and *joie de vivre* of countless men and boys. A juicy steak is no less valuable to an African villager than to a banker in Zurich, his consumption is no less significant, socially and economically for being tacitly unmentionable. Because the activity is mostly illegal it has been largely disregarded in socio-economic surveys by official bodies (i.e. FAO, UNDP and national commissions). Such analyses ignore an important dimension of rural life and a resource that would be of measurable economic and dietary significance were the protein to be replaced from domestic sources. The loss of all wild herbivores in the "cordon sanitaire" zone of South-western Tanzania has resulted in intensive hunting of rats, birds and even insectivorous bats (Volume II) such is the desire for meat. Game of this size is generally ignored in areas where antelopes are still available.

If initiatives for the systematic exploitation of African wildlife resources are to have any long-term future it will be necessary to understand the scale, the extent and the ecological role of hunting in the villages and districts. Furthermore, strategies will have to involve and satisfy people at these levels as well as at strata that are of more obvious political significance.

The value of an animal is related to the economic level of the people who exploit it and to how those people use it. Such exploitation is conditioned by a few physical and geo-political realities or constraints which differ greatly at the three major levels of small locality, nation and world

community. Animal resources are viewed from different perspectives at each level. The diversity of uses to which animal communities can be put proliferates at each level. The actual costs increase as more technology, transport and overheads are involved but the relative costs tend to decline.

At each stratum the increasing diversity of interests in wildlife products is vested in a smaller proportion of the community as the scale increases. (There is a corresponding increase in the diversity of conflicting interests.)

The products emanating from wildlife cost more in the higher strata but if films, scientific data, tourist-generating publicity etc. are regarded as "products" from wildlife they involve no costs at the local level. When local consumption of wildlife is below or equal to natural increment there is also a model economy but the practical costs of abundant wildlife in the countryside are far from negligible.

Costs and benefits differ fundamentally between the local and higher levels and the table opposite indicates some of these differences.

This chart suggests that demands and interests are more numerous at the international and national levels but that costs are relatively higher at local and national levels. Perhaps ways should be found whereby international interests in African wildlife and its products could offset this imbalance by subsidies, particularly for research and investment in sustained yield exploitation. The scale of research and investment needed before wildlife can be exploited in a systematic way is completely beyond the means of hard-pressed East African governments. Some of the more obvious prerequisites for rational exploitation are as follows: 1. An inventory of species and their present distribution. 2. The numbers of major large mammal species, population by population. 3. Local distribution patterns and movements. 4. Habitat, diet and space requirements at the individual and population levels. 5. Age and sex structures within specific populations and their population dynamics. 6. Recent history of population changes and reasons for fluctuations. 7. The role of diseases. 8. The influence of humans and cattle on community structures and vice-versa. 9. Documentation of growth and maturation rates, carrying capacity, sustainable yield and biomass per unit area is needed for species and communities under various conditions.

In addition to such biological base-line knowledge there needs to be more than usual attention to marketing, economic and management plans, study of interactions or conflict with other development projects and alternative land uses. Also study of how rural inhabitants would participate in the activities and share revenue. Numerous small-scale or pilot schemes have been attempted and have faced overwhelming problems particularly in marketing and in opposition from livestock interests but they have proved that cropping can be economically viable.

The productivity of African savanna herbivores has been shown to be very high and biomasses range between about 7 kg/ha in sub-desert to nearly 300 kg/ha in western Uganda moist savannas. Efficient livestock rearing needs continuous water control, fencing, manipulation and planting of vegetation as well as intensive attention to disease and health. For the exploitation of wildlife to realize its potential, equally sustained and probably more costly and complex ecological study will be needed, particularly in

STRATA	LOCAL GROUND LEVEL	NATIONAL	INTERNATIONAL
Those with sustained economic interests in wild mammals	Fresh-meat hunters landowners, traders, transport owners guides, trappers	Preserved meat processors sporting firms and clubs Traders; ivory, skin and transport/tourist firms. Tourist trade hotelliars and airlines, live animal trade, zoos, research faculties Photographic retailers	Preserved meat importers Photographic Trade, Media and Information Industry. Biological supply Houses
Products	fresh meat raw ivory hides	Preserved meat, ivory products and trophies, skins and leather Live animal "magnets" for tourists Material for scientific research	Focal material for tourists, sporting photographic and other trades
Benefits	revenue from products, fresh meat	protein products employment recreation trade diversification taxes increased contacts	preserved products access to material, information and animals
Costs or constraints	destruction of crops, fences etc. Disease Restriction on land use for other purposes	Pest and disease control Damages Preservation and processing costs	Subsidies? Transport Duties Fluctuating demand

the initial phases. Continuous monitoring is essential.

In this last respect small aircraft have revolutionized wildlife management. Wildlife stocks can now be treated as a quantifiable resource which can be monitored repeatedly, reliably and cheaply. They also emphasize that

the wildlife resources of Africa are finite. Radio-tracking has also transformed the study of movement and range patterns while immobilizing drugs have simplified control and translocation, particularly of large or dangerous animals.

Wildlife management, particularly in the Americas, has become a specialized profession with an extensive literature. Pioneering work is also being conducted in many African countries by a wide range of scientists. This commentary can do little more than stress the need for support while the maps and profiles have underlined the urgency. An acknowledged asset will go to waste without substantial long-term investment. Yet the time needed for basic research and the building up of viable production units must still be measured in tens of years. International and bilateral aid agreements look for much quicker returns and so have generally failed to support such research. Where funds have been offered Governments have sometimes lacked the interest or the will to take advantage of them.

Many herbivores of comparable size to cattle are suited to harvesting at one to one-and-a-half years yet cattle are seldom slaughtered economically at less than two-and-a-half years. Even short-term returns may be better served by wildlife in the end! The herbivores with the highest potential for intensive exploitation appear to be hippopotamus, giant hog, kob, puku, lechwe, gazelles, impala and topi. Many others, including elephant, zebra and buffalo may also be productive in suitable areas and in combination with other species. The principal rationale for the exploitation of large herbivores in Africa should be their highly diversified and efficient use of indigenous habitats. Conservation is a separate issue but land-use patterns are such that many potential cropping areas are likely to be part of larger wildlife complexes adjacent to or even within national parks. The reconciliation of conservation (as the primary purpose of a national park) with cropping raises issues in which local geography, the scale of specific animal populations in space and time, regional land allocation patterns, local and national politics all play crucial roles. In spite of potential conflicts the interests of national parks and future exploitation will both be best served by stepping up the intensity of ecological research in all major African habitats, particularly savannas and flood plains.

Research in the Galana, Nanyuki, Laikipia, Rift Valley and Kitengela areas of Kenya, Aswa-Lolim in Uganda, Loliondo and Yaida Chini in Tanzania has provided some foundations for experimental game ranching or sustained yield cropping. Controlled hunting areas are other potential localities but little can be expected without major investment, commitment and further sustained research.

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Checklist of species with authorities

(Scientific names only listed in the order followed in preceding volumes)

- Homo sapiens* Linnaeus 1758
Pan gorilla Savage and Wyman 1847
Pan troglodytes Blumenbach 1779
Colobus badius Kerr 1792
Colobus polycomos Zimmerman 1780
Colobus abyssinicus Oken 1816 (*C. guereza* Rüppell 1835)
Papio cynocephalus Linnaeus 1766
Cercocebus albigena Gray 1850
Cercocebus galeritus Peters 1879
Cercopithecus aethiops Linnaeus 1758
Cercopithecus (cephus) ascanius Audebert 1799
Cercopithecus (l'hoesti) l'hoesti Sclater 1898
Cercopithecus (nictitans) mitis Wolff 1822
Cercopithecus (mona) denti Thomas 1907
Cercopithecus neglectus Schlegel 1829
Cercopithecus hamlyni Pocock 1907 (addendum)
Cercopithecus (Erythrocebus) patas Schreber 1774
Perodicticus potto Müller 1766
Galago crassicaudatus Geoffroy 1812
Galago demidovii Smith 1833
Galago zanzibaricus Matschie 1893
Galago senegalensis Geoffroy 1796
Galago inustus Schwarz 1930
Procavia johnstoni Thomas 1894
Procavia habessinica Hemprich and Ehrenberg 1832
Heterohyrax brucei Gray 1868
Dendrohyrax validus True 1890
Dendrohyrax arboreus Smith 1827
Dendrohyrax dorsalis Fraser 1852
Manis gigantea Illiger 1815
Manis temmincki Smuts 1832
Manis tricuspis Rafinesque 1820
Orycteropus afer Pallas 1766
Dugong dugon Müller 1776
Micropotamogale ruwenzori de Witte and Frechkop 1955
Potamogale velox Du Chaillu 1860
Chrysochloris stuhlmanni Matschie 1894
Erinaceus albiventris Wagner 1841
Rhynchocyon cirnei Peters 1847
Petrodromus tetradactylus Peters 1846
Elephantulus rufescens Peters 1878
Elephantulus brachyrhynchus Smith 1836
Elephantulus fuscipes Thomas 1894
Myosorex blarina Thomas 1906
Myosorex zinki Heim de Balsac and Lamotte 1956
Myosorex geata Allen and Loveridge 1927
Myosorex norae Thomas 1906
Myosorex polulus Hollister 1916
Sylvisorex lunaris Thomas 1906
Sylvisorex granti Thomas 1907
Sylvisorex suncoides Osgood 1936
Sylvisorex megalura Jentink 1888
Scutisorex somereni Thomas 1910
Suncus murinus Linnaeus 1766
Suncus lixus Thomas 1898
Suncus varilla Thomas 1895
Paracrociodura schoutedeni Heim de Balsac 1956
Crociodura maurisca Thomas 1904
Crociodura littoralis Heller 1910
Crociodura monax Thomas 1910
Crociodura ultima Dollman 1915
Crociodura niobe Thomas 1906
Crociodura fumosa Thomas 1904
Crociodura luna Dollman 1910
Crociodura turba Dollman 1910
Crociodura zimmeri Osgood 1936
Crociodura nigricans Bocage 1889
Crociodura hildegardeae Thomas 1904
Crociodura roosevelti Heller 1910
Crociodura bicolor Bocage 1889
Crociodura planiceps Heller 1910
Crociodura nana Dobson 1890
Crociodura allex Osgood 1910
Crociodura bottegi Thomas 1898
Crociodura nanilla Thomas 1909
Crociodura pasha Dollman 1915
Crociodura somalica Thomas 1895
Crociodura flavescens Geoffroy 1827
Crociodura hirta Peters 1852
Crociodura silacea Thomas 1895
Crociodura jacksoni Thomas 1904
Crociodura denti Dollman 1915
Crociodura smithi Thomas 1895
Crociodura boydi Dollman 1915
Crociodura katherina Kershaw 1922
Crociodura voi Osgood 1910

- Crocidura butleri* Thomas 1911
Crocidura sururæ Heller 1910
Crocidura macartheri St Ledger 1934
Crocidura zaphiri Dollman 1915
Rousettus aegyptiacus Geoffroy 1810
Stenonycteris lanosus Thomas 1906
Lissonycteris angolensis Bocage 1898
Myonycteris torquata Dobson 1878
Pteropus comorensis Nicoll 1808
Pteropus voeltzkowi Matschie 1909
Eidolon helvum Kerr 1792
Epomophorus labiatus Temminck 1837
Epomophorus anurus Heuglin 1864
Epomophorus crypturus Peters 1852
Epomophorus wahlbergi Sundevall 1846
Micropteropus pusillus Peters 1867
Epomops franqueti Tomes 1860
Plerotes anchietæ Seabra 1900
Hypsignathus monstrosus Allen 1861
Megaloglossus woermanni Pagenstecher 1885
Coleura afra Peters 1852
Taphozous mauritanus Geoffroy 1818
Taphozous perforatus Geoffroy 1818
Taphozous hildegardeæ Thomas 1909
Taphozous nudiventris Cretzschmar 1826
Taphozous peli Temminck 1853
Rhinopoma hardwickei Gray 1831
Nycteris hispida Schreber 1775
Nycteris grandis Peters 1871
Nycteris aethiopica Dobson 1878
Nycteris macrotis Dobson 1876
Nycteris thebaica Geoffroy 1818
Nycteris arge Thomas 1903
Nycteris nana Andersen 1912
Cardioderma cor Peters 1872
Lavia frons Geoffroy 1810
Rhinolophus ruwenzori Hill 1942
Rhinolophus hildebrandti Peters 1878
Rhinolophus fumigatus Rüppell 1842
Rhinolophus clivosus Cretzschmar 1828
Rhinolophus darlingi Andersen 1905
Rhinolophus alcyone Temminck 1852
Rhinolophus landeri Martin 1838
Rhinolophus blasii Peters 1866
Rhinolophus simulator Andersen 1904
Rhinolophus swinnyi Gough 1908
Hipposideros megalotis Heughlin 1861
Hipposideros abae Allen 1917
Hipposideros commersoni Geoffroy 1813
Hipposideros cyclops Temminck 1853
Hipposideros camerunensis Eisentraut 1956
Hipposideros caffer Sundevall 1846
Hipposideros ruber Noack 1893
Asellia tridens Geoffroy 1818
Cloeotis percivali Thomas 1901
Triænopis persicus Dobson 1871
Myotis welwitschii Gray 1866
Myotis tricolor Temminck 1832
Myotis bocagei Peters 1870
Pipistrellus nanus Peters 1852
Pipistrellus nanulus Thomas 1904
Pipistrellus kuhli Natterer 1817
Pipistrellus rueppelli Fischer 1829
Pipistrellus rusticus Tomes 1861
Pipistrellus permixtus Aellen 1957
Eptesicus tenuipinnis Peters 1872
Eptesicus rendalli Thomas 1889
Eptesicus loveni Granvik 1924
Eptesicus pusillus Leconte 1858
Eptesicus somalicus Thomas 1901
Eptesicus capensis Smith 1829
Mimetillus moloneyi Thomas 1891
Laeophotis wintoni Thomas 1901
Nycticeius hirundo de Winton 1899
Nycticeius albofuscus Thomas 1890
Nycticeius schlieffeni Peters 1859
Scotophilus gigas Dobson 1875
Scotophilus nigrita Schreber 1774
Scotophilus leucogaster Cretzschmar 1826
Glauconycteris variegata Tomes 1861
Glauconycteris gleni Peterson and Smith 1973
Glauconycteris superba Hayman 1939
Glauconycteris humeralis Allen 1917
Glauconycteris argentata Dobson 1875
Kerivoula argentata Tomes 1861
Kerivoula harrisoni Thomas 1901
Kerivoula smithi Thomas 1880
Kerivoula cuprosa Thomas 1912
Kerivoula africana Dobson 1878
Miniopterus minor Peters 1867
Miniopterus inflatus Thomas 1901
Miniopterus schreibersi Kuhl 1819
Myopterus whitleyi Scharff 1900
Tadarida lobata Thomas 1891
Tadarida africana Dobson 1876
Tadarida fulminans Thomas 1903
Tadarida aegyptiaca Geoffroy 1818
Tadarida ansorgei Thomas 1913
Tadarida major Trouessart 1897
Tadarida bemmeleni Jentink 1879
Tadarida nigeriæ Thomas 1913
Tadarida bivittata Heuglin 1861

- Tadarida aloysiisabaudiae* Feste 1907
Tadarida pumila Cretzschmar 1831
Tadarida chapini Allen 1917
Tadarida nanula Allen 1917
Tadarida brachypterus Peters 1852
Tadarida midas Sundevall 1843
Tadarida congica Allen 1917
Tadarida trevori Allen 1917
Tadarida demonstrator Thomas 1913
Tadarida condylura Smith 1833
Tadarida niveiventer Cabrera and Ruxton 1926
Tadarida thersites Thomas 1903
Tadarida leonis Thomas 1908
Tadarida acetabulosus Hermann 1804
Platymops setiger Peters 1878
Otomops martiensseni Matschie 1897
Lepus capensis Linnaeus 1758
Lepus crawshayi de Winton 1899
Lepus whytei Thomas 1894
Poelagus majorita St Leger 1932
Pronolagus rupestris Smith 1834
Funisciurus pyrrhopus Cuvier 1833
Funisciurus carruthersi Thomas 1906
Funisciurus lucifer Thomas 1897
Funisciurus vexillarius Kershaw 1923
Funisciurus palliatus Peters 1852
Funisciurus cepapi Smith 1836
Funisciurus ochraceus Huet 1880
Funisciurus boehmi Reichenow 1886
Funisciurus alexandri Thomas and Wroughton 1907
Funisciurus flavittis Peters 1852
Heliosciurus ruwenzori Schwann 1907
Heliosciurus gambianus Ogilby 1822
Heliosciurus rufobrachium Waterhouse 1842
Protoxerus stangeri Waterhouse 1842
Xerus rutilus Cretzschmar 1826
Xerus erythropus Geoffroy 1803
Anomalurus derbianus Gray 1842
Anomalurus pusillus Thomas 1887
Anomalurus beecrofti Fraser 1852
Idiurus zenkeri Matschie 1894
Pedetes capensis Forster 1778
Cryptomys ochraceocinereus Heuglin 1864
Cryptomys hottentotus Lesson 1826
Cryptomys mechowii Peters 1881
Heliophobius argenteocinereus Peters 1852
Heterocephalus glaber Rüppell 1842
Tachyoryctes splendens Rüppell 1835
Tatera valida Bocage 1890
Tatera inclusa Thomas and Wroughton 1908
Tatera robusta Cretzschmar 1826
Tatera nigricauda Peters 1878
Tatera leucogaster Peters 1852
Tatera boehmi Noack 1887
Taterillus emini Thomas 1892
Gerbillus gerbillus Olivier 1801
Gerbillus harwoodi Thomas 1901
Gerbillus pusillus Peters 1878
Lophiomyia imhausi Milne-Edwards 1867
Dendromus nyikae Wroughton 1909
Dendromus melanotis Smith 1834
Dendromus mesomelas Brants 1827
Dendromus mystacalis Heuglin 1863
Deomys ferrugineus Thomas 1888
Steatomys pratensis Peters 1846
Steatomys opimus Pousargues 1894
Steatomys minutus Thomas 1905
Beamys hindei Thomas 1909
Cricetomys gambianus Waterhouse 1840
Cricetomys emini Wroughton 1910
Saccostomus campestris Peters 1846
Delanymys brooksi Hayman 1962
Otomys orestes Thomas 1900
Otomys typus Heuglin 1877
Otomys denti Thomas 1906
Otomys anchietae Bocage 1882
Otomys angoniensis Wroughton 1906
Otomys irroratus Brants 1827
Rattus rattus Linnaeus 1758
Rattus norvegicus Berkenhout 1769
Praomys fumatus Peters 1878
Praomys natalensis Smith 1834
Praomys pernanus Kershaw 1921
Praomys delectorum Thomas 1910
Praomys jacksoni de Winton 1897
Praomys denniae Thomas 1906
Praomys aeta Thomas 1911
Praomys stella Thomas 1911
Aethomys chrysophilus de Winton 1897
Aethomys kaiseri Noack 1887
Aethomys hindei Thomas 1902
Aethomys longicaudatus Tullberg 1893
Mus tenellus Thomas 1903
Mus minutoides Smith 1834
Mus triton Thomas 1909
Mus bufo Thomas 1906
Mus musculus Linnaeus 1758
Dasymys incomptus Sundevall 1847
Mylomys dybowski Pousargues 1893
Hybomys univittatus Peters 1876

- Rhabdomys pumilio* Sparrmann 1784
Lemniscomys griselda Thomas 1904
Lemniscomys striatus Linnaeus 1758
Lemniscomys macculus Thomas and Wroughton 1910
Lemniscomys barbarus Linnaeus 1758
Pelomys minor Cabrera and Ruxton 1926
Pelomys fallax Peters 1852
Pelomys isseli de Beaux 1924
Arvicanthis niloticus Desmarest 1822
Arvicanthis lacernatus Rüppell 1842
Thallomys paedulus Sundevall 1846
Thamnomys rutilans Peters 1876
Thamnomys venustus Thomas 1907
Grammomys dolichurus Smuts 1832
Grammomys cometes Thomas and Wroughton 1908
Grammomys macmillani Wroughton 1907
Oenomys hypoxanthus Pucheran 1855
Lophuromys sikapusi Temminck 1853
Lophuromys flavopunctatus Thomas 1888
Lophuromys woosmani Thomas 1906
Uranomys ruddi Dollman 1909
Acomys dimidiatus Cretzschmar 1826
Acomys cahirinus Geoffroy 1803
Acomys spinosissimus Peters 1852
Acomys subspinosus Waterhouse 1838
Zelotomys hildegardae Thomas 1902
Colomys goslingi Thomas and Wroughton 1907
Malacomys longipes Milne-Edwards 1877
Graphiurus murinus Desmarest 1822
Atherurus africanus Gray 1842
Hystrix africae-australis Peters 1852
Hystrix cristata Linnaeus 1758
Thryonomys swinderianus Temminck 1827
Thryonomys gregorianus Thomas 1894
Canis aureus Linnaeus 1758
Canis adustus Sundevall 1846
Canis mesomelas Schreber 1775
Lycaon pictus Temminck 1820
Otocyon megalotis Desmarest 1822
Ictonyx striatus Perry 1810
Poecilogle albinucha Gray 1864
Mellivora capensis Schreber 1776
Lutra maculicollis Lichtenstein 1835
Aonyx congica Lönnberg 1910
Aonyx capensis Schinz 1821
Genetta genetta Linnaeus 1758
Genetta tigrina Schreber 1778
Genetta servalina Pucheran 1855
Genetta victoriae Thomas 1901
Poiana richardsoni Thomas 1842
Osbornictis piscivora Allen 1919
Civettictis civetta Schreber 1778
Viverricula indica Geoffroy 1838
Nandinia binotata Gray 1830
Herpestes ichneumon Linnaeus 1758
Herpestes naso de Winton 1901
Herpestes sanguineus Rüppell 1835
Helogale parvula Sundevall 1846
Helogale hirtula Thomas 1904
Dologale dybowskii Pousargues 1894
Atilax paludinosus Cuvier 1777
Mungos mungo Gmelin 1788
Crossarchus alexandri Thomas and Wroughton 1907
Ichneumia albicauda Cuvier 1829
Rhynchogale melleri Gray 1865
Bdeogale crassicauda Peters 1852
Bdeogale nigripes Pucheran 1855
Crocota crocata Erxleben 1777
Hyaena hyaena Linnaeus 1758
Proteles cristatus Sparrman 1783
Felis sylvestris Linnaeus 1758
Felis serval Schreber 1777
Felis caracal Schreber 1776
Felis aurata Temminck 1827
Felis pardus Linnaeus 1758
Felis leo Linnaeus 1758
Acinonyx jubatus Schreber 1775
Loxodonta africana Blumenbach 1797
Diceros bicornis Linnaeus 1758
Ceratotherium simum Burchell 1817
Equus grevyi Oustalet 1882
Equus asinus Linnaeus 1758
Equus caballus Linnaeus 1758
Equus quagga Gmelin 1788
Potamochoerus porcus Linnaeus 1758
Hylochoerus meinertzhageni Thomas 1904
Phacochoerus aethiopicus Pallas 1767
Hippopotamus amphibius Linnaeus 1758
Camelus dromedarius Linnaeus 1758
Hyemoschus aquaticus Ogilby 1840
Giraffa camelopardalis Linnaeus 1772
Okapia johnstoni Sclater 1901
Bos taurus Linnaeus 1758
Bubalus bubalis Linnaeus 1758
Syncerus caffer Sparrman 1779
Tragelaphus spekei Sclater 1864
Tragelaphus scriptus Pallas 1766
Tragelaphus imberbis Blyth 1869

<i>Tragelaphus strepsiceros</i> Pallas 1766	<i>Cephalophus dorsalis</i> Gray 1846
<i>Taurotragus derbianus</i> Gray 1847	<i>Cephalophus monticola</i> Thunberg 1789
<i>Taurotragus oryx</i> Pallas 1766	<i>Sylvicapra grimmia</i> Linnaeus 1758
<i>Boocercus eurycerus</i> Ogilby 1837	<i>Redunca fulvorufula</i> Afzelius 1815
<i>Neotragus batesi</i> de Winton 1903	<i>Redunca redunca</i> Pallas 1777
<i>Neotragus moschatus</i> von Dueben 1846	<i>Redunca arundinum</i> Boddaert 1785
<i>Raphicerus sharpei</i> Thomas 1897	<i>Kobus vardonii</i> Livingstone 1857
<i>Raphicerus campestris</i> Thunberg 1811	<i>Kobus kob</i> Erxleben 1777
<i>Ourebia ourebi</i> Zimmerman 1783	<i>Kobus ellipsiprymnus</i> Ogilby 1833
<i>Oreotragus oreotragus</i> Zimmerman 1783	<i>Gazella thomsoni</i> Gunther 1884
<i>Madoqua saltiana</i> Desmarest 1816	<i>Gazella granti</i> Brooke 1872
<i>Madoqua kirki</i> Günther 1880	<i>Gazella semmerringii</i> Cretzschmar 1826
<i>Madoqua guentheri</i> Thomas 1894	<i>Litocranius walleri</i> Brooke 1878
<i>Cephalophus adersi</i> Thomas 1918	<i>Aepyceros melampus</i> Lichtenstein 1812
<i>Cephalophus natalensis</i> Smith 1834	<i>Beatragus hunteri</i> Sclater 1889
<i>Cephalophus harveyi</i> Thomas 1893	<i>Damaliscus lunatus</i> Burchell 1823
<i>Cephalophus nigrifrons</i> Gray 1871	<i>Alcelaphus buselaphus</i> Pallas 1766
<i>Cephalophus rubidus</i> Thomas 1901	<i>Connochaetes taurinus</i> Burchell 1823
<i>Cephalophus rufilatus</i> Gray 1846	<i>Hippotragus equinus</i> Desmarest 1804
<i>Cephalophus leucogaster</i> Gray 1873	<i>Hippotragus niger</i> Harris 1838
<i>Cephalophus callipygus</i> Peters 1876	<i>Oryx gazella</i> Linnaeus 1758
<i>Cephalophus spadix</i> True 1890	<i>Ovis aries</i> Linnaeus 1758
<i>Cephalophus sylvicultor</i> Afzelius 1815	<i>Capra hircus</i> Erxleben 1777



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Miles

Gazetteer



Achwa (see Aswa-Lolim)
 Addo Cape South Africa
 Akagera (Kagera) National Park Rwanda
 Aswan S. Egypt
 Azande S.W. Sudan
 Bangwelu basin N. Zambia
 Benone Cameroon
 Bourbandjidah Cameroon
 Broken Hill (Kabwe) Zambia
 Bugalla Island Lake Victoria $0^{\circ} 20' S 32^{\circ} 15' E$
 Chapota S.W. Tanzania $8^{\circ} 15' S 31^{\circ} 15' E$
 Chobe W. Uganda $2^{\circ} 12' N 32^{\circ} 12' E$
 Chua district N. Uganda
 Dufle Uganda $3^{\circ} 35' N 31^{\circ} 55' E$
 Elandsfontein South Africa
 Faro Cameroon
 Fort Warwick C. Kenya $1^{\circ} 18' N 36^{\circ} 46' E$
 Galana River E. Kenya $3^{\circ} 6' S 40^{\circ} 8' E$
 Garamba National Park N.E. Zaire
 Gatara C. Kenya $1^{\circ} 9' N 36^{\circ} 54' E$
 Gemmeiza S. Sudan
 George Lake W. Uganda $0^{\circ} 30' 10' E$
 Hanang Mt C. Tanzania $4^{\circ} 26' S 35^{\circ} 25' E$
 Ijara E. Kenya $2^{\circ} 23' N 40^{\circ} 33' E$
 Ilengwa N.W. Uganda $3^{\circ} 38' N 31^{\circ} 12' E$
 Inde N.W. Uganda $2^{\circ} 47' N 31^{\circ} 18' E$
 Issaua River C. Tanzania $6^{\circ} 38' S 34^{\circ} 8' E$
 Jozani S. Zanzibar $6^{\circ} 20' S 39^{\circ} 35' E$
 Juba River S. Somalia
 Kabalega National Park W. Uganda
 Kafue National Park Zambia
 Kahuzi Mt Rwanda

Karoo Cape S. Africa
 Kassala N.E. Sudan
 Katwe W. Uganda $0^{\circ} 3' S 29^{\circ} 45' E$
 Kedong C. Kenya $1^{\circ} S 36^{\circ} 36' E$
 Kekopey C. Kenya $0^{\circ} 27' S 36^{\circ} 18' E$
 Kericho W. Kenya $0^{\circ} 24' S 35^{\circ} 16' E$
 Kibbish Omo Valley Ethiopia
 Kikagati S. Uganda $1^{\circ} S 30^{\circ} 40' E$
 Kikuyu scarp C. Kenya $1^{\circ} S 36^{\circ} 34' E$
 Kinangop C. Kenya $0^{\circ} 34' S 36^{\circ} 44' E$
 Kirawira N. Tanzania $2^{\circ} 8' S 34^{\circ} E$
 Kiwengwa E. Zanzibar $6^{\circ} 12' S 39^{\circ} 34' E$
 Kondoa district C. Tanzania
 Kongwa C. Tanzania $6^{\circ} 8' S 36^{\circ} 28' E$
 Koobi Fora E. Turkana Kenya $3^{\circ} 57' N 36^{\circ} 11' E$
 Kordofan district N.W. Sudan
 Kruger National Park South Africa
 Laikipia district C. Kenya
 Laisamis C. Kenya $1^{\circ} 33' N 37^{\circ} 46' E$
 Lema downs C. Kenya $0^{\circ} 13' N 37^{\circ} 18' E$
 Lerai Ngorongoro Tanzania $3^{\circ} 10' S 35^{\circ} 35' E$
 Lira N. Uganda $2^{\circ} 11' N 32^{\circ} 54' E$
 Loliondo N. Tanzania $2^{\circ} 2' S 35^{\circ} 36' E$
 Loreze N.W. Uganda $30^{\circ} 28' N 31^{\circ} 44' E$
 Lorian E. Kenya $0^{\circ} 40' N 39^{\circ} 30' S$
 Loskop South Africa
 Luangwa E. Zambia
 Makokou Gaboon
 Manda Island E. Kenya $2^{\circ} 15' S 40^{\circ} 55' E$
 Mandera N.E. Kenya $3^{\circ} 57' N 41^{\circ} 52' E$
 Maralal C. Kenya $1^{\circ} 6' N 36^{\circ} 41' E$
 Matathia C. Kenya $0^{\circ} 59' S 36^{\circ} 38' E$
 Matheniko district N.E. Uganda
 Matopos National Park Zimbabwe
 Mekambo Gaboon
 Melkbos South Africa
 Midigo N.W. Uganda $3^{\circ} 36' N 31^{\circ} 14' E$
 Mkomazi N.E. Tanzania $4^{\circ} 15' S 38^{\circ} 28' E$
 Mongalla S. Sudan
 Mzima Springs S.E. Kenya $2^{\circ} 59' S 38^{\circ} 2' E$
 Nabilatuk E. Uganda $1^{\circ} 56' N 34^{\circ} 57' E$
 Narus River N.E. Uganda $3^{\circ} 40' N 33^{\circ} 44' E$
 Ngangerabeli plains E. Kenya $1^{\circ} 35' S 40^{\circ} 20' E$
 Ngorora N. Kenya $0^{\circ} 55' N 36^{\circ} 11' E$
 Nkosi E. Lake Victoria $0^{\circ} 44' S 32^{\circ} 16' E$
 Nyamugasani River W. Uganda $0^{\circ} 6' S 29^{\circ} 50' E$
 Nyeri C. Kenya $0^{\circ} 26' S 36^{\circ} 56' E$
 Ogaden E. Ethiopia
 Olgarwa Shambalai N. Tanzania $4^{\circ} 5' S 36^{\circ} 9' E$

Pibor plains S. Sudan
 Rabongo W. Uganda $2^{\circ} 6' N 31^{\circ} 58' E$
 Rama Addei Somalia
 Rumuruti C. Kenya $0^{\circ} 18' N 36^{\circ} 31' E$
 Rutshuru-Rwindi plains E. Zaire
 Rwana plains N. Tanzania $2^{\circ} 2' S 34^{\circ} 15' E$
 Saiwa W. Kenya $1^{\circ} 8' N 35^{\circ} 9' E$
 Samburu district N. Kenya
 Sankabor C. Ethiopia
 Senegambia region West Africa
 Sengwa N.W. Zimbabwe
 Seronera N. Tanzania $2^{\circ} 22' S 34^{\circ} 52' E$
 Shimba hills N.R. S.E. Kenya $4^{\circ} 16' S 39^{\circ} 25' E$
 Shira plateau N. Tanzania $3^{\circ} 3' S 37^{\circ} 14' E$
 Shungura Omo River S.E. Ethiopia
 Simien Ethiopia
 Singida district C. Tanzania
 Sudd swamp region S. Sudan
 Togore N. Tanzania $2^{\circ} 56' S 55^{\circ} 14' E$
 Trans-Nzoia district Kenya
 Uasin-Gishu district W. Kenya
 Ukambani district C. Kenya
 Upemba National Park S.E. Zaire
 Uplands C. Kenya $1^{\circ} 3' S 36^{\circ} 39' E$
 Wamba C. Kenya $0^{\circ} 59' N 37^{\circ} 18' E$
 Yathabara C. Kenya $0^{\circ} 16' S 36^{\circ} 46' E$
 Yaounde C. Cameroon

Systematic Index

A

Aardvaark 613, 614
Addax 541
Aegodonta 15
Aepyceros 11, 21, 167, 438 *et seq.*, 588
 melampus 460 *et seq.*
Alcelaphine 5, 11, 12, 29 *et seq.*, 167, 168,
 337, 396, 438 *et seq.*, 630
Alcelaphini 8, 11, 15, 19, 20, 38, 51, 159
 et seq., 438 *et seq.*, 639
Alcelaphus 21, 31, 36, 169, 438 *et seq.*,
 506
 buselaphus 45, 443 *et seq.*, 502 *et seq.*
 buselaphus 443, 444
 caama 443, 444, 451, 507
 cokei 443, 444, 503 *et seq.*
 jacksoni 503
 keniae 503
 kongoni 503
 lelwel 443 *et seq.*, 503 *et seq.*
 lichtensteini 166, 441 *et seq.*, 503 *et*
 seq.
 major 443, 444, 446, 447, 507
 nakurrae 503
 ritchiei 503
 swaynei 443, 444, 451, 507
 tora 443, 444, 507
Ammodorcas 164, 396, 539
Antelope 3 *et seq.*, 159 *et seq.*, 396 *et seq.*
 dwarf 172
 gazelline 14, 394 *et seq.*
 horse (*Hippotragus equinus*) 568, 569
 horse-like 539
 neotragine 22, 172 *et seq.*
 pigmy (*Neotragus batesi*) 26, 174, 186
 et seq., 267, 569
 pronghorn 2
 roan (*Hippotragus equinus*) 19, 31, 74,
 534, *et seq.*, 628, 633
 sable (*Hippotragus niger*) 19, 29 *et seq.*,
 162, 163, 542 *et seq.*, 628 *et seq.*
 spiral-horned 49

Anthracothere 2
Antidorcas 11, 168, 396
Antidorcine 14, 15, 17, 167, 396
Antilocapra 231
Antilopinae 1, 8, 12 *et seq.*, 159 *et seq.*
Antilopine 12, 29, 48, 49, 164
Antilopini 11, 14, 18, 19, 20, 159 *et seq.*,
 394 *et seq.*
Ape 610
Artiodactyl 3 *et seq.*
Artiodactyla 56 *et seq.*
Aurochs (*Bos primigenius*) 52

B

Baboon 609, 610, 611
Banteng (*Bos javanicus*) 52
Bat 617, 618, 619
 fruit-eating 617, 618, 619
 hammer (*Hypsignathus*) 618
 heart-nosed (*Cardioderma*) 618
 insectivorous 619
 nectar-eating 617, 618
 vampire 617
Beatragus 21, 438 *et seq.*, 477
 antiquus 477
 hunteri 439, 476 *et seq.*
Beira (*Dorcotragus*) 168, 172, 173
 Somali (*Dorcotragus megalotis*) 174
Blesbok (*Damaliscus dorcas*) 451
Blesmol 621
Bongo (*Boocercus eurycerus*) 19 *et seq.*,
 142 *et seq.*
Bontebok (*Damaliscus*) 168
Boocercus 21, 38, 39, 51, 72
 eurycerus 78, 80, 142, 143
 nakuae 78
Boodonta 15
Bos 50, 52, 55
 gaurus 52
 javanicus 52
 mutus 52
 primigenius 52, 55

taurus 54
 Boselaphine 9, 12, 78
 Boselaphini 9, 11, 49
Boselaphus 8, 9, 49, 78
 Bovid 1 *et seq.*
 Bovidae 1, 5 *et seq.*
 Bovinae 1 *et seq.*
 Bovine 12, 48 *et seq.*
 Bovini 8, 9, 11, 19, 48 *et seq.*
Bubalus 52
 bubalis 52, 55, 60
 Buffalo 7 *et seq.*
 African (*Syncerus caffer*) 19, 56 *et seq.*
 Asiatic water (*Bubalus bubalis*) 52, 55, 60
 Cape (*Syncerus c. caffer*) 57 *et seq.*, 633
 forest (*Syncerus caffer nanus*) 57 *et seq.*
 mountain (*Syncerus caffer matheusi*) 63
 savanna (*see* buffalo, Cape)
 water 168
 Bushbuck (*Tragelaphus scriptus*) 7, 18, 30, 32, 44, 72 *et seq.*, 94 *et seq.*, 200, 273, 632, 638
 Bushduiker 200
 Bushpig 633

C

Canid 624, 626, 639
 Cape hunting dog 624
Capra 168, 590, 591
 falconeri 77
Capricornis 590
 Caprine 12, 14, 17, 29, 163, 164, 176, 543, 588 *et seq.*
 Caprini 8, 11, 14, 19, 159, 162, 164, 168, 541, 543, 588 *et seq.*
Cardioderma 618
 Carnivora 624
 Carnivore 20, 624 *et seq.*, 637, 639
 Cat 625, 626
 Cattle (*Bos taurus*) 1 *et seq.*
 Cephalophine 14, 176, 263 *et seq.*
 Cephalophini 8, 11, 17, 19, 159, 160, 174, 263, 267, 276
Cephalophus 17, 21, 263 *et seq.*
 adersi 16, 268, 271, 274 *et seq.*, 286 *et seq.*
 callipygus 264, 268 *et seq.*, 304 *et seq.*
 barbertoni 305
 callipygus 279, 305
 lestradei 278, 305
 weynsi 278, 279, 305, 307

dorsalis 7, 11, 26, 267 *et seq.*, 293, 314 *et seq.*
harveyi 262, 268 *et seq.*, 296 *et seq.*
ignifer 279, 305
jentinki 276, 279, 309
leucogaster 268, 274 *et seq.*, 289 *et seq.*
maxwelli 271, 283, 285
monticola 11, 17, 21, 263 *et seq.*, 280 *et seq.*
 aequatorialis 281
 hecki 281
 lugens 281, 282
 pembae 281, 282
 schusteri 281
 sundevalli 281, 288
natalensis 17, 268, 272 *et seq.*, 294 *et seq.*
 harveyi 288
niger 276, 279
nigrifrons 267 *et seq.*, 300 *et seq.*
 fosteri 301
 hooki 278, 297, 301
 kivuensis 278, 292, 293, 301, 302
 nigrifrons 278
ogilbyi 274, 276, 277
rubidus 268, 274 *et seq.*, 292 *et seq.*
ruflatus 268, 274 *et seq.*, 290 *et seq.*
 rubidior 291
spadix 268, 274, 276, 305 *et seq.*
sylvicultor 4, 268 *et seq.*, 307 *et seq.*
zebra 274, 276, 277, 295, 317

Cercopithecus mitis 279
 Cervid 7, 27
 Cervoid 6, 7
 Chamois (*Rupicapra*) 590
 Cheetah 624, 639
 Chevrotain 3, 4, 27
 Chimpanzee 611
 Chiroptera 617
Chlorocichla laetissima 105
 Chousingha (*Tetracerus*) 49, 50, 77
 Chrysochloridae 615
 Civet 624
 palm 625
Connochaetes 21, 169, 438 *et seq.*
 gnou 448, 451, 524 *et seq.*
 taurinus 451, 453
 albojubatus 452, 525, 529
 johnstoni 452, 525
Cuniculus 263

D

Damalisc 29, 37, 453, 454

- Damaliscine 443
Damaliscus 21, 168, 169, 438 *et seq.*
 dorcas 498
 lunatus 440, 448, 458, 477, 484 *et seq.*
 jimela 485
 korrigum 485
 lunatus 442, 485 *et seq.*
 lyra 485
 purpurescens 485
 tiang 485
 topi 485
Dasyprocta 263
 Deer 2, 4
Dendrohyrax arboreus 279
 dorsalis 279
Dibitag (Ammodorcas) 164, 337, 396
Dik-dik (Madoqua) 9, 13 *et seq.*, 161, 172
 et seq., 241 *et seq.*, 629
 Kirk's 632
 Dog 639
Dolichotis 37
Dorcopsis 263
Dorcopsulus 263
Dorcotragus 160, 168, 172 *et seq.*
 megalotis 174, 185
 Dormouse 621
 Dugong 614, 615
 Duiker 7 *et seq.*, 160, 162, 263 *et seq.*, 629,
 630
 Abbot's (*Cephalophus spadix*) 306,
 307
 Ader's (*Cephalophus adersi*) 286, 287
 bay 26, 314, 315
 blue (*Cephalophus monticola*) 280 *et*
 seq.
 black-fronted (*Cephalophus nigri-*
 frons) 300, 301
 bush (*Sylvicapra grimmia*) 171, 276,
 318 *et seq.*
 common (*Sylvicapra grimmia*) 318,
 319
 dwarf red (*Cephalophus adersi*) 286,
 287
 grey 632
 Harvey's red (*Cephalophus harveyi*)
 296 *et seq.*
 Natal red (*Cephalophus natalensis*)
 294, 295, 298
 Peter's (*Cephalophus callipygus*) 304,
 305
 red 17, 274, 279, 291 *et seq.*
 red-flanked (*Cephalophus rufilatus*) 290, 291
 Ruwenzori red (*Cephalophus rubidus*)
 292
 striped (*Cephalophus zebra*) 317
 white-bellied (*Cephalophus leucogas-*
 ter) 289
 yellow-backed (*Cephalophus sylvicul-*
 tor) 4, 279, 308, 309, 312

 E
 Eland (*Taurotragus*) 12, 19, 20, 43 *et seq.*,
 72 *et seq.*, 630 *et seq.*
 common (*Taurotragus oryx*) 77, 82,
 123 *et seq.*
 Derby's (*Taurotragus derbianus*) 77,
 82, 122 *et seq.*
 giant 125
 Elephant 65, 636 *et seq.*
 African 627, 633
 Elephant shrew 615
 Eotragine 14, 17, 49, 164, 174
Eotragus 10 *et seq.*, 174
 clavata 16
 sansaniensis 16
 Equid 2, 7, 630, 638, 639
 Erinacidae 615

 F
 Felid 624, 638, 639
 Flying-squirrel 621, 623

 G
 Galago 612
 Gaur (*Bos gaurus*) 52
 Gayal 52
Gazella 10, 11, 164, 396 *et seq.*
 (*Nanger*) 394, 398, 423
 (*Procapra*) 398
 albonotata 403
 dama 398, 423, 424
 granti 21, 394, 398 *et seq.*
 brighti 415, 417
 granti 415, 417
 petersi 415, 417
 robertsi 415, 417
 rufifrons 403
 soemmeringii 21, 394, 398, 416, 422
 et seq.
 berberana 425
 butteri 422
 thomsoni 21, 158, 394, 398 *et seq.*
 nasalis 403
 thomsoni 403
 Gazelle 12, 14, 17, 37 *et seq.*, 394 *et seq.*,
 629, 644

- Grant's (*Gazella granti*) 31, 33, 400, 401, 408, 414 *et seq.*, 632
 Soemmering's (*Gazella soemmeringii*) 422 *et seq.*
 Thomson's (*Gazella thomsoni*) 29, 158, 400 *et seq.*, 632
 Gazelline 14, 15, 167
 Gemsbok (*Oryx g. gazella*) 168, 582, 587
 Genet 624
 Gerbil 621
 Gerenuk (*Litocranius walleri*) 29, 30, 47, 170, 396, 397, 426 *et seq.*, 630
 Giraffe 2, 170, 629, 630, 631, 633
 Giraffe-antelope (*Litocranius*) 396
 Gnu (*Connochaetes taurinus*) 19, 29, 37, 44, 64, 438, 451 *et seq.*, 524 *et seq.*, 639
 brindled 450, 451
 Goat (*Capra*) 1 *et seq.*, 159 *et seq.*, 540, 543, 588 *et seq.*
 Golden mole 615
 Gorilla 609 *et seq.*
 Grysbok 16, 35, 203, 206
 Cape (*Raphicerus melanotis*) 174, 203
 Sharpe's (*Raphicerus sharpei*) 3, 6, 202 *et seq.*, 241
 Guenon (*Cercopithecus*) 21, 22, 41, 610, 611
- H
- Hare 620
 Hartebeest (*Alcelaphus buselaphus*) 22 *et seq.*, 166, 351, 438 *et seq.*, 502 *et seq.*
 Hunter's (*Beatragus hunteri*) 439, 476 *et seq.*
 red 450
 Hedgehog 615, 616
Hemitragus 590
 Herbivore 2 *et seq.*
 Hippopotamus 3, 64, 629, 630, 644
 Hippotragine 12, 29, 163, 164, 337, 539 *et seq.*
 Hippotragini 8, 11, 15, 19, 51, 159 *et seq.*, 539 *et seq.*
Hippotragus 168, 541, 543, 544
 bohlini 11, 539
 equinus 21, 539, 540, 543, 568 *et seq.*
 bakeri 569
 langheldi 569
 niger 21, 35, 538, 539, 549, 552 *et seq.*
 kirki 555, 556
 niger 555
 roosevelti 555, 556
 Hirola (*Beatragus*) 438, 454, 476 *et seq.*
 Hog, giant 644
 Horse 7
 Hyaena, 38, 70, 624
 Hyaenid 624, 639
Hydropotes 231
Hylarnus harrisoni (see *Neotragus batesi harrisoni*)
Hypsignathus 618
 Hyracoid 2
 Hyracoidea 613
 Hyrax 241, 637
- I
- Illingoceros* 78
 Impala 18 *et seq.*, 74, 164, 165, 167, 337, 438, 439, 453, 457, 460 *et seq.*, 636, 644
 black faced 450
 Insectivora 613, 615, 616, 619
- J
- Jackal 639
- K
- Klipspringer (*Oreotragus oreotragus*) 27, 35, 177, 183, 184, 203, 231 *et seq.*
 Kob (*Kobus kob*) 18, 29, 30, 44, 164, 165, 167, 331, 332, 351, 366 *et seq.*, 630, 644
Kobus 328 *et seq.*
 adenota 21, 328, 329
 ellipsiprymnus 21, 328 *et seq.*, 384 *et seq.*
 defassa 380, 385
 ellipsiprymnus 385
 kob 21, 164, 328 *et seq.*, 366 *et seq.*
 kob 331
 leucotis 331, 367
 thomasi 331, 367
 leche 328, 329, 333, 339
 megaceros 328, 329, 333, 339, 380
 vardoni 328, 329, 336, 339, 368, 382, 383
 Kongoni 18, 139, 458, 502, 503, 505, 633
 Kudu 22, 30, 33, 45, 74, 77, 115 *et seq.*
 giant 20, 80
 greater (*Tragelaphus strepsiceros*) 43, 45, 74, 76 *et seq.*, 115 *et seq.*, 633
 lesser (*Tragelaphus imberbis*) 1, 19, 22, 38, 40, 72, 73, 79, 83, 106 *et seq.*, 632

Kudu-eland group 30

L

Lagomorph 7, 636, 639

Lechwe 332, 338, 644

Nile (*Kobus megaceros*) 339

Leopard 639

Leporidae 620

Leptobos 11

Lion 639

Litocranius 21, 47, 50, 164, 394, 396, 397,

433

walleri 394, 426 et seq.

M

Macroscelididae 615

Madoqua 11, 14, 15, 21, 160 et seq., 242

et seq., 543

guentheri 9, 13, 26, 174, 242 et seq.

kirkii 26, 161, 174, 183, 244 et seq.

damarensis 246

kirkii 245

saltiana 174, 184, 244 et seq.

phillipsi 251, 254, 255

swaynei 245

Mangabey 610

Markhor (*Capra falconeri*) 77

Mazama 263

Megachiroptera 617

Megalotragus 168

Megalovis 11

Mesembriportax 11, 77

Microchiroptera 617

Microtragus 540

Miotragocerus 11

Mole rat 621

Mongoose 38

Monkey 640

colobus 610, 611

patas 609

vervet 609, 611

Mouse 622

Muntiacus 263

Muntjac (*Muntiacus*) 27

Murid 21

Muridae 22

Mustelid 624

Myoprocta 263

N

Neotragine 3, 11, 14 et seq., 162, 164, 172 et seq.

Neotragini 8, 11, 12, 17, 19, 20, 159 et seq.

Neotragus 17, 21, 160 et seq., 203, 264,

265, 462, 543

batesi 16, 17, 26, 174 et seq., 186 et seq., 265, 266

batesi 186

harrisoni 186, 187, 188, 191

moschatus 160, 173 et seq., 192 et seq., 265

pygmaeus 174, 176, 187, 191, 265, 266

Nilghai (*Boselaphus*) 49, 50

Nototragus 203

Nyala (*Tragelaphus angasi*) 78, 85

O

Oiocerus 10

Oiocerus tanyceras 588

Okapi 633

Oreamnos 540

americanus 540

Oreotragus 11, 21, 27, 160, 171, 172, 174,

177, 184, 185, 203

oreotragus 231, 234

aceratos 231, 235

aureus 231, 234, 235

centralis 231, 235, 236

oreotragus 231, 235

porteousi 235

saltatrixoides 231, 235

schillingsi 231, 234, 235

somalicus 231, 235

Oribi (*Ourebia ourebi*) 16, 22 et seq., 171

et seq., 217 et seq., 337

Oryx (*Oryx*) 18, 21, 29, 31, 35, 37, 38,

168, 169, 541 et seq., 579 et seq., 630

beisa 630, 632

Oryx 541

gazella 539, 550, 551, 579 et seq.

beisa 545, 578, 579, 582

callotis 579, 582

gazella 582, 587

leucoryx 587

sivalensis 11

Otomys 639

Otter shrew 615

Ourebia 16, 21, 23 et seq., 160, 172 et seq.,

217 et seq.

ourebia 217 et seq.

aequatoria 217

cottoni 217

haggardi 217

hastata 217

kenyae 217

masakensis 217

Ovibovini 11, 14, 589, 590
Ovis 590, 591, 639
 ammon 591
 hodgsoni 591
 poli 591
 Ox, wild (*Bos primigenius*) 52
 Oxen (*Bos taurus*) 52 et seq.

P

Pachytragus 10, 11
Palaeoryx major 540
 pallasi 540
Pan gorilla beringei 595
 Pangolin 613, 614
Panthalops 396
Parmularius 11, 443, 477
 altidens 477
Pelea 24, 25, 160, 174, 539
 capreolus 23, 26, 160
Pelorovis 11, 52, 60, 64
 antiquus 60
 Perissodactyla 628
 Pholidota 613
 Pig 629, 630, 639
 Porcupine 621, 623
 Potamogalidae 615
 Potto 612
 Primates 609 et seq., 637, 638
 Proboscid 2
 Proboscidea 627
 Prongbuck (*Antilocapra*) 50, 231
 Prosimian 610, 611
Prostrepsiceros 11
Protoryx carolinae 540
 crassicorne 540
 longipes 540
Protragocerus 10
 labidotus 78
Pseudotragus 10, 540
Pudu 263
Puku (*Kobus vardoni*) 332, 336, 337, 341, 351, 382, 383, 644

R

Rabaticeros 442, 443
 Rabbit 620
Raphicerus 170, 172, 185
 campestris 21, 160, 170, 174, 203 et seq.
 neumanni 209
 melanotis 16, 17, 174, 185
 sharpei 3, 6, 21, 174, 200 et seq.

Rat 621, 636
 cane 621, 623
 crested 623
Redunca 11, 328 et seq.
 arundinum 21, 328 et seq., 345, 351, 358 et seq.
 fulvorufula 16, 21 et seq., 328 et seq., 342 et seq.
 chanleri 343
 redunca 21, 328 et seq., 345, 350 et seq.
 bohor 331
 cottoni 331, 351, 356
 donaldsoni (see *cottoni*)
 nigeriensis 331
 redunca 331
 tohi (see *wardi*)
 ugandae (see *wardi*)
 wardi 331, 351
 Reduncine 11, 14, 22 et seq., 176, 328 et seq.
 Reduncini 8 et seq., 51, 159, 162, 163, 174, 328 et seq.
 Reedbuck 18, 30 et seq., 162, 328 et seq.
 common 343, 632
 bohor (*Redunca redunca*) 331, 350 et seq.
 mountain (*Redunca fulvorufula*) 22, 23, 26, 170, 329 et seq., 342 et seq.
 southern (*Redunca arundinum*) 340, 360 et seq.
Rhabdomys 639
 Rhebuck, Cape (*Pelea capreolus*) 23, 160
 Rhinoceros 629, 641
 black 633
 white 633
Rhynchocyon 37
Rhynchotragus 246
 Rodent 20, 621 et seq., 638, 639
 Rodentia 621
 Ruminant 2 et seq.
Rupicapra 590
 Rupicaprine 590
 Rupicaprini 11, 14, 589, 590

S

Saiga 396
 tartarica 249
 Sciuridae 22
Selenoportax vexillarius 78
 Serow (*Capricornis*) 590
 Sheep 1 et seq., 159 et seq., 588 et seq.
 merino 1

Shrew 615, 617
 Sirenia 614, 615
 Sitatunga (*Tragelaphus spekei*) 18, 30,
 32, 44, 72, 75, 83 *et seq.*, 632
 Soricidae 615
 Springbok (*Antidorcas*) 168, 462
 Spring-hare 621, 623
 Squirrel 621, 623, 639
 Steinbuck (*Raphicerus campestris*) 203,
 208 *et seq.*
 Suni 22, 43, 162, 173 *et seq.*, 192 *et seq.*
 Sylvicapra 21, 263, 270, 272, 273, 276,
 320
 grimmia 264, 318 *et seq.*
 abyssinica 319
 altifrons 319
 altivallis 319
 coronata 319
 deserti 319
 grimmia 319
 hindei 319
 lobeliarum 319
 lutea 319
 nyansae 319
 ocularis 319
 orbicularis 319
 roosevelti 319
 splendidula 319
 steinhardti 319
 uvirensis 319
 Syncerus 11, 52, 60 *et seq.*
 caffer 9, 21, 56 *et seq.*
 brachyceros 60, 63, 64
 caffer 56 *et seq.*
 mathewsi 57, 63, 64
 nanus 57, 61, 63

T

Tahr (*Hemitragus*) 590
 Tapir 2
 Taurotragus 11, 21, 48, 72
 derbianus 79, 80, 122 *et seq.*
 oryx 21, 77, 79, 80, 123 *et seq.*
 Tenrec 615
 Tetracerus 8, 49, 50, 77
 Tetrameryx 78
 Tommy (*Gazella thomsoni*) 403 *et seq.*
 Topi 18, 31, 351, 438, 450 *et seq.*, 633,
 644
 Tragelaphine 3, 11, 12, 33, 35, 37, 43, 72
 et seq., 630

Tragelaphini 8, 9, 11, 19, 42, 48 *et seq.*
 Tragelaphus 50, 51, 72, 78
 angasi 78, 80, 85
 arkelli 80
 buxtoni 80
 gaudreyi 11, 79
 imberbis 1, 21, 40, 51, 72, 73, 79, 80,
 106 *et seq.*
 nakuae 11, 78, 79
 scriptus 21, 23, 51, 80, 94, 96
 barkeri 95
 heterochrous 95
 '*scriptus*' 95, 98
 '*sylvaticus*' 95, 98
 spekei 11, 21, 32, 51, 78, 80, 84 *et seq.*
 gratus 85
 larkeni 85
 selousi 85
 spekei 85
 sylvestris 86
 strepsiceros 21, 45, 51, 76, 79, 80, 115
 et seq.
 grandis 79, 80
 maryanus 79
 Tragulid 2, 21
 Tragulidae 5
 Traguline 5
 Traguloid 7
 Tree hyrax 21
 Tubulidentata 613
 Tylopod 7

U

Ugandax 11, 52, 60, 61
 gautieri 60
 Ungulate 64, 626, 628 *et seq.*
 horned 1, 62

V

Viverrid 624, 639
 Vole 622

W

Walangania 10
 Warthog 633
 Waterbuck (*Kobus ellipsiprymnus*) 12,
 19, 29, 31, 74, 328, 332, 337, 340,
 384 *et seq.*, 633

Waterdeer (*Hydropotes*) 231

Wild ass, Somali 633

Wildebeest (*Connochaetes taurinus*) 524,
525, 527, 633

blue 628

Y

Yak (*Bos mutus*) 52

Z

Zebra 38, 64, 628 *et seq.*

Zebu 12, 52, 54

Subject Index

A

Activity patterns

- blue duiker 283, 285
- bohor reedbuck 351, 353, 357
- bongo 148, 149, 152 *et seq.*
- buffalo 64
- bush duiker 322
- bushbuck 97, 99, 102
- Cephalophus adersi* 287
- dorsalis* 317
- natalensis* 295
- nigrifrons kivuensis* 301, 302
- rubidus* 293
- rufilatus* 291
- spadix* 307
- sylvicultor* 310
- dik-dik 252, 253
- duiker 268, 270
- gerenuk 436
- gnu 527, 530
- hartebeest 511
- hippotragine 545
- hirola 481
- impala 468
- klipspringer 237, 238
- kob 371 *et seq.*
- lesser kudu 111
- mountain reedbuck 346
- oribi 222, 227
- oryx 583
- pigmy antelope 188, 189
- puku 383
- roan antelope 571, 573
- Reduncini 332, 333
- sable antelope 559, 560
- Sharpe's grysbok 205
- sitatunga 87
- southern reedbuck 346
- sun 196
- tommy 408
- topi 497
- waterbuck 386, 387

Adaptation

- Alcelaphini 438 *et seq.*
- Antilopini 14 *et seq.*
- bovid 7 *et seq.*
- Caprini 14, 588, 589
- duiker 264 *et seq.*
- gazelle 394 *et seq.*
- gerenuk 427 *et seq.*
- hippotragine 540 *et seq.*
- Redunca fulvorufula* 328 *et seq.*
- Reduncini 328 *et seq.*
- tragelaphine 74, 83

Aggression

- bushbuck 102
- dik-dik 254, 255
- eland 133, 136, 137
- hartebeest 515, 517
- oribi 227, 228
- roan antelope 574
- sable antelope 560
- sun 198, 201

Alarm posture

- buffalo 68

Appeasement behaviour

- buffalo 68
- dik-dik 254, 255

B

Birth

- Grant's gazelle 420
- roan antelope 576
- steinbuck 215
- sun 199

Birth peak

- Alcelaphus buselaphus cokei* 513
- lelwel* 514
- blue duiker 284
- bongo 151
- bush duiker 326
- bushbuck 103
- eland 137
- gnu 536

- Grant's gazelle 418, 420
- hippotragine 548
- hirola 482
- impala 474
- klipspringer 239
- kob 380
- lesser kudu 112
- mountain reedbuck 348
- oribi 228
- pigmy antelope 191
- puku 383
- roan antelope 575
- Sharpe's grysbok 206, 207
- sitatunga 93
- Soemmering's gazelle 424
- southern reedbuck 348
- steinbuck 215
- suní 199
- Thomson's gazelle 410
- Brain
 - Cephalophini 267
 - duiker 267
 - neotragine 267
- Breeding season
 - alcelaphine 458
 - Alcelaphus buselaphus cokei* 513, 514
 - lelwel* 514
 - blue duiker 284
 - bohor 358
 - bongo 155
 - buffalo 70
 - bush duiker 326
 - dik-dik 258
 - gerenuk 437
 - Grant's gazelle 420
 - greater kudu 120
 - hippotragine 548
 - hirola 482
 - impala 471, 472, 474
 - klipspringer 239
 - kob 369, 380
 - lesser kudu 112
 - mountain reedbuck 348
 - oribi 228
 - oryx 585
 - pigmy antelope 191
 - puku 383
 - red-flanked duiker 291
 - roan antelope 575
 - sable antelope 564
 - Sharpe's grysbok 206
 - sitatunga 93
 - Soemmering's gazelle 424
 - southern reedbuck 364
 - steinbuck 215
 - suní 199
 - Thomson's gazelle 410
 - topi 493, 494
 - waterbuck 393
 - yellow-backed duiker 313
- C
 - Camouflage
 - bushbuck 72, 95, 104
 - dik-dik 251
 - eland 72
 - klipspringer 231
 - lesser kudu 107
 - Sharpe's grysbok 205
 - sitatunga 72
 - tragelaphine 72
 - Captivity, diet
 - Carnivora 625, 626
 - Chiroptera 618, 619
 - elephant 627
 - hare 620
 - Insectivora 615, 616
 - Pholidota 613, 614
 - Primates 610, 611
 - Rodentia 621, 622
 - Sirenia 615
 - Tubulidentata 613, 614
 - ungulate 629, 630
 - Captivity, housing
 - Carnivora 624
 - Chiroptera 618
 - elephant 627
 - Insectivora 616
 - Primates 611
 - Rodentia 621
 - ungulate 628, 629
 - Captivity, management
 - Carnivora 624 *et seq.*
 - Chiroptera 617, 618, 619
 - Hyracoidea 613
 - Insectivora 615, 616, 617
 - Leporidae 620
 - Pholidota 613
 - Primates 609 *et seq.*
 - Proboscidea 627, 628
 - Rodentia 621, 622, 623
 - Sirenia 614, 615
 - Tubulidentata 613, 614
 - ungulate 628 *et seq.*
 - Captivity, pests and diseases
 - Carnivora 625

- Chiroptera 618
- elephant 627
- Proboscidea 627
- Rodentia 622
- ungulate 630, 631
- Captivity, sedation and anaesthetization
 - Carnivora 626, 627
 - Chiroptera 619
 - elephant 627, 628
 - hare 620
 - herbivores 632, 633
 - Insectivora 616, 617
 - Pholidota 614
 - Primates 611, 612, 613
 - Rodentia 622, 623
 - Sirenia 615
 - Tubulidentata 614
 - ungulate 629, 631, 632
- Captivity, success
 - buffalo 70
 - bush duiker 327
 - bushbuck 105
 - Carnivora 624, 625
 - Cephalophus adersi* 288
 - callipygus* 305
 - Chiroptera 617
 - elephant 627
 - greater kudu 121
 - hare 620
 - hartebeest 522
 - Insectivora 615
 - lesser kudu 113
 - roan antelope 577
 - Rodentia 622
 - Sirenia 614
 - sitatunga 93
 - ungulates 628
- Chromosome number
 - Cephalophini 170
 - Raphicerus campestris* 170
- Climbing
 - blue duiker 283
- Coat pattern
 - alcelaphine 450
 - black faced impala 450
 - brindled gnu 450
 - Gazella soemmeringi* 450
 - red hartebeest 450
 - topi 450
- Colouration
 - agrimi goat 169
 - Alcelaphini 169
 - Alcelaphus* 451
 - Antilopini 168, 169
 - beira 168
 - blesbok 451
 - blue duiker 282
 - bongo 143, 149
 - bontebok 168
 - bushbuck 72, 101
 - Caprini 168, 169
 - Cephalophus adersi* 287
 - callipygus* 305
 - lestradei* 305
 - weynsi* 305
 - dorsalis* 315
 - harveyi* 297, 299
 - leucogaster* 289
 - natalensis* 295
 - nigrifrons* 301
 - fosteri* 301
 - hooki* 301
 - kivuensis* 301
 - nigrifrons* 301
 - rubidus* 292
 - rufilatus* 291
 - spadix* 307
 - sylvicultor* 309
 - Cercopithecus* 169
 - common eland 123, 127, 136
 - Damaliscus* 451
 - lunatus* 485
 - Derby's eland 123
 - dik-dik 251
 - Dorcotragus* 169
 - duiker 274
 - eland 72
 - Gazella granti* 415
 - soemmeringii* 423
 - thomsoni* 403
 - gemsbok 168
 - generuk 433, 462
 - gnu 451
 - goat 168
 - hartebeest 506, 520
 - Hippotragini 168, 169
 - hirola 477
 - impala 462
 - klipspringer 231, 235, 236
 - Kobus ellipsiprymus* 385
 - kob* 367
 - lesser kudu 107
 - Neotragini 168
 - oribi 217
 - oryx 169, 579, 580
 - pigmy antelope 187

- Redunca arundinum* 361
fulvorufula 343
redunca 351, 361
Reduncini 339, 340
roan antelope 569
sable antelope 555, 556
sitatunga 72
springbok 168
steinbuck 209
suni 193
Sylvicapra 320
grimmia deserti 319
nyansae 319
orbicularis 319
roosevelti 319
topi 451
tragelaphine 72
Tragelaphus scriptus 95 *et seq.*
gratus 85
selousi 85
spekei 85
- Communication, scent
alcelaphine 448, 449, 450
antelope 35
black fronted duiker 302
blue duiker 285
bohor reedbuck 358
bush duiker 324
bushbuck 99, 102, 103
dik-dik 177 *et seq.*, 255 *et seq.*
duiker 271
eland 134 *et seq.*
gazelle 395, 396
gerenuk 436
gnu 530
Grant's gazelle 401, 416
grysbok 35
hippotragine 548
impala 463, 465, 466
klipspringer 239
kob 370, 375
neotragine 177 *et seq.*
oribi 180 *et seq.*, 217 *et seq.*
pigmy antelope 190
Reduncini 333, 337, 338
sitatunga 89
Soemmering's gazelle 424
southern reedbuck 362, 363
suni 196, 197
Thomson's gazelle 401, 409
topi 494, 495, 496
tragelaphine 74
waterbuck 385 *et seq.*
- Communication, sound
Alcelaphini 457
antelope 35
black fronted duiker 302
blue duiker 283
bohor reedbuck 358
bongo 150
buffalo 44
bushbuck 99
dik-dik 183, 253, 257
duiker 272
eland 136
gerenuk 436
gnu 529
greater kudu 121
hartebeest 521, 522
impala 462, 466, 467
klipspringer 183, 238, 239
lesser kudu 111
mountain reedbuck 348
neotragine 183
oribi 183, 228
pigmy antelope 191
red flanked duiker 291
Reduncini 338
reedbuck 339
sable antelope 566
sitatunga 89
southern reedbuck 362, 363
suni 196, 199
topi 497
tragelaphine 74
yellow backed duiker 312
- Communication, visual 38 *et seq.*
alcelaphine 454
Alcelaphini 457
antelope 31 *et seq.*
bovid 33 *et seq.*
buffalo 64
Cephalophus monticola 272, 283
dik-dik 184
duiker 272
eland 134, 136
gnu 37
Grant's gazelle 401, 415, 416
guenon 41
hartebeest 37, 506, 517, 519
hippotragine 548
impala 462
Madoqua 185
mountain reedbuck 348
neotragine 183
Neotragus 185

- oribi 217, 218
- oryx 37
- Raphicerus* 185
- Reduncini 338, 339
- reedbuck 338, 339
- Thomson's gazelle 401, 407
- topi 496
- tragelaphine 72 *et seq.*
- waterbuck 387
- Competition
 - bovid 2
 - buffalo 67
 - eland 82, 83
- Conservation areas 604 *et seq.*
- Conservation aspects
 - alcelaphine 459
 - bongo 156, 157
 - Cephalophus adersi* 288
 - rufilatus* 291
 - Dorcotragus megalotis* 185
 - hirola 480, 481, 483
 - neotragine 185
 - Raphicerus melanotis* 185
 - Redunca fulvorufula* 343
 - roan antelope 577
- Copulation
 - blue duiker 284
 - bohor reedbuck 358
 - bongo 155
 - buffalo 70
 - bush duiker 326
 - bushbuck 103
 - dik-dik 259
 - gerenuk 436
 - gnu 536
 - Grant's gazelle 420
 - greater kudu 120
 - hartebeest 520
 - impala 474
 - kob 380
 - oribi 228
 - oryx 585
 - sable antelope 565
 - sitatunga 93
 - Soemmering's gazelle 425
 - southern reedbuck 365
 - Thomson's gazelle 410
 - topi 500
- Courtship
 - Alcelaphus buselaphus cokei* 521
 - lelwel* 521
 - blue duiker 284, 285
 - bohor reedbuck 358
 - bongo 155
 - bovid 46
 - bush duiker 324, 325, 326
 - bushbuck 103
 - dik-dik 259
 - duiker 272
 - eland 134, 137
 - gnu 536
 - Grant's gazelle 420
 - greater kudu 120
 - hartebeest 519, 520
 - impala 460, 461, 474
 - klipspringer 240
 - kob 380
 - lesser kudu 111
 - mountain reedbuck 348
 - oribi 228
 - oryx 585
 - roan antelope 575
 - sable antelope 561, 564, 565
 - sitatunga 93
 - Soemmering's gazelle 424, 425
 - southern reedbuck 364, 365
 - steinbuck 215
 - sun 196
 - Thomson's gazelle 410
 - topi 493, 499
 - waterbuck 392, 393

D

Defence

- blue duiker 283
- bohor reedbuck 358
- bongo 43, 74, 150, 154
- buffalo 68, 69
- bush duiker 320
- bushbuck 99, 103, 104
- dik-dik 253
- duiker 270
- eland 43, 72, 74, 130, 133
- gemsbok 587
- gerenuk 436
- gnu 534, 535
- greater kudu 43, 115
- hartebeest 514, 517
- impala 464, 465
- klipspringer 238
- oribi 221, 228
- oryx 545, 587
- Peter's duiker 305
- Reduncini 332
- roan antelope 576
- sable antelope 561, 566

- Sharpe's grysbok 205, 206
- steinbuck 211 *et seq.*
- sun 196, 200
- tommy 407, 408, 412
- tragelaphine 43, 72, 74
- waterbuck 332, 391, 392, 393
- Dentition
 - Aegodonta 15
 - Alcelaphini 15
 - Boodonta 15
 - bovid 7
 - Bovinae 15
 - Cephalophini 17, 267
 - Cephalophus adersi* 16
 - dorsalis* 17, 26
 - monticola* 17
 - duiker 267
 - Eotragus clavata* 16
 - sansaniensis* 16
 - Hippotragini 15, 539, 540, 541
 - Madoqua guentheri* 26
 - Neotragini 267
 - Neotragus* 176
 - batesi* 16, 17, 26
 - Ourebia* 16
 - Raphicerus melanotis* 16, 17
 - Redunca fulvorufula* 16
 - Reduncini 15, 16
 - white bellied duiker 289
- Dewlap
 - eland 127, 132
- Diet
 - Alcelaphini 51
 - antelope 7
 - Antilopini 396
 - bay duiker 316, 317
 - black fronted duiker 302
 - blue duiker 282, 283
 - bohor reedbuck 351, 353
 - bongo 144, 145, 148
 - bovid 1 *et seq.*
 - Bovini 51
 - buffalo 58, 59, 65
 - bush duiker 322
 - bushbuck 97
 - Caprini 589
 - Cephalophus dorsalis* 26
 - nigrifrons* 26
 - common eland 127, 128, 129
 - Derby's eland 124, 125
 - dik-dik 251, 252
 - duiker 20, 267, 268, 269
 - eland 80, 81
 - equid 7
 - gerenuk 170, 427, 434, 435
 - giraffe 170
 - gnu 452, 525
 - Grant's gazelle 417, 418
 - greater kudu 116, 117
 - hartebeest 22, 452, 508, 509
 - hippotragine 540, 543, 548
 - Hippotragini 51
 - hirola 481
 - impala 462, 469
 - klipspringer 236
 - kob 369
 - kudu 80, 81
 - lagomorph 7
 - lesser kudu 22, 110
 - Madoqua guentheri* 26
 - kirkii* 26
 - mountain reedbuck 22, 24, 345, 346
 - Natal red duiker 295
 - Neotragus batesi* 17, 26
 - oribi 22 *et seq.*, 220, 221
 - oryx 582, 583
 - Pelea* 24
 - capreolus* 26
 - Peter's duiker 305
 - pigmy antelope 188
 - puku 353, 383
 - Redunca fulvorufula* 26
 - Reduncini 51, 328 *et seq.*
 - roan antelope 571, 573
 - sable antelope 557, 558
 - Sharpe's grysbok 205, 207
 - sitatunga 87
 - Soemmering's gazelle 423
 - southern reedbuck 362
 - steinbuck 210
 - sun 22, 43, 194, 195
 - tommy 404
 - topi 353, 488, 490
 - tragelaphine 72
 - tragulid 21
 - waterbuck 385, 386
 - white bellied duiker 289
 - yellow-backed duiker 310
- Digestion
 - ruminant 5 *et seq.*
- Digestive system
 - pecoran 5
 - ruminant 5 *et seq.*
 - Tragulidae 5
- Disability, survival with
 - buffalo 64, 69

- bushbuck 100
- Diseases and parasites 634 *et seq.*
 - blue duiker 283
 - bongo 155, 156
 - bushbuck 99, 105
 - common eland 141
 - Derby's eland 125
 - gazelle 399
 - giant eland 125
 - gnu 535, 536
 - greater kudu 121
 - hartebeest 522
 - klipspringer 241
 - lesser kudu 112
 - mountain reedbuck 348
 - sitatunga 89, 90
 - topi 498
 - waterbuck 392
- Disease transmission 634, 635
 - Rodentia 622
 - vampire bat 617
- Display
 - alcelaphine 454
 - Antilopinae 169
 - bohor reedbuck 356, 357
 - bongo 149
 - bovid 46
 - bush duiker 325
 - bushbuck 101
 - chamois 590
 - common eland 124, 129, 134
 - Connochaetes taurinus albojubatus* 452
 - johnstoni* 452
 - Derby's eland 124
 - gnu 451, 531, 533
 - Grant's gazelle 33, 400, 419
 - greater kudu 120
 - hartebeest 515, 518 *et seq.*
 - impala 462, 466 *et seq.*
 - kob 377, 378, 380
 - kudu 82
 - lesser kudu 111
 - mountain reedbuck 348
 - oryx 38, 580, 581
 - puku 383
 - Reduncini 333
 - roan antelope 574, 575
 - sable antelope 556, 563
 - southern reedbuck 362 *et seq.*
 - springbok 462
 - Thomson's gazelle 400, 401, 406 *et seq.*
 - topi 496
 - tragelaphine 74
 - Tragelaphus scriptus* 95
 - waterbuck 389, 390
- Distress call
 - buffalo 68, 69
- Distribution
 - Aepyceros melampus* 461, 462
 - Alcelaphus buselaphus* 508, 510
 - caama* 507
 - cokei* 503, 507
 - lelwel* 503, 507
 - lichtensteini* 503, 507
 - major* 507
 - swaynei* 507
 - tora* 507
 - Beatragus hunteri* 480, 481
 - bongo 144
 - Bos primigenius* 55
 - buffalo 57, 66
 - bushbuck 95 *et seq.*
 - Caprini 588
 - Cephalophus adersi* 277, 287
 - callipygus* 297
 - barbertoni* 305
 - callipygus* 279, 305
 - lestradei* 305
 - weynsi* 279, 305
 - dorsalis* 317
 - harveyi* 278, 297, 301
 - jentinki* 309
 - leucogaster* 277, 289
 - monticola* 267, 283
 - aequatorialis* 281
 - hecki* 281
 - lugens* 281
 - pembae* 281
 - schusteri* 281
 - sundevalli* 281
 - natalensis* 17, 295, 297
 - niger* 305
 - nigrifrons* 278, 301
 - ogilbyi* 277
 - rubidus* 292, 293
 - rufilatus* 291
 - spadix* 307, 309
 - sylvicultor* 309
 - common eland 128, 129, 139, 140
 - Connochaetes taurinus* 525, 526
 - albojubatus* 525
 - johnstoni* 525
 - Damaliscus lunatus* 488, 489
 - jimela* 485
 - korrigum* 485

- lunatus* 485
- lyra* 485
- purpurescens* 485
- tiang* 485
- topi* 485
- Derby's eland 123, 124, 125
- dik-dik 247
- duiker 274 *et seq.*
- Gazella granti* 400, 416, 417
 - brighti* 415, 417
 - gazella* 415, 417
 - petersi* 415, 417
 - robertsi* 415, 417
- soemmeringii* 416, 423, 424
- butteri* 423
- thomsoni* 400, 403, 404
 - nasalis* 403, 404
 - thomsoni* 403, 404
- greater kudu 115, 116
- hippotragine 540 *et seq.*
- Hippotragus equinus bakeri* 569
- langheldi* 569
- klipspringer 234, 235
- Kobus ellipsiprymnus* 385, 386
 - defassa* group 385
 - ellipsiprymnus* group 385
 - kob* 367, 368
 - leucotis* 367
 - thomasi* 367
 - vardoni* 368, 383
- lesser kudu 107, 108
- Litocranius walleri* 433
- Madoqua guentheri* 245 *et seq.*
 - kirkii* 245 *et seq.*
 - saltiana* 245 *et seq.*
- Neotragini 177
- Neotragus* 187
 - batesi* 187, 188
 - moschatus* 187
 - pygmaeus* 187
- oribi 217, 220, 221
- Oryx gazella* 582
 - beisa* 579
 - callotis* 579
 - gazella* 579
- Raphiceros melanotis* 17
- red duiker 276, 278
- Redunca arundinum* 345, 351, 361
- Redunca fulvorufula* 343, 345
- Redunca redunca* 345, 351, 353, 361
 - cottoni* 356
- roan antelope 546, 569, 570
- sable antelope 546, 556, 557
- Sharpe's grysbok 205
- sitatunga 90, 91, 93
- steinbuck 209, 210
- sun 194
- Sylvicapra grimmia* 319, 321
- Syncerus caffer* 62
 - brachyceros* 63
 - caffer* 57, 63
 - mathewsi* 57
 - nanus* 57, 63
- Tragelaphus scriptus* 96
 - imberbis* 107, 108
 - spekei* 88
 - gratus* 85
 - selousi* 85
 - spekei* 85
 - strepsiceros* 115, 116
- Divergence
 - antidorcine 14 *et seq.*
 - Antilopinae 8 *et seq.*
 - Antilopini 20, 395, 396
 - boselaphine 12, 17
 - bovid 7 *et seq.*
 - eotragine 17
 - neotragine 17
 - tragelaphine 78
- Diversification
 - Antilopini 396, 398
 - Bovidae 7 *et seq.*
- Diversity
 - duiker 274 *et seq.*
- Domestication
 - Bos javanicus* 52
 - mutus* 52
 - primigenius* 52
 - bovid 1 *et seq.*
 - Bubalus bubalis* 52
 - buffalo 53, 70
 - gayal 52
 - ox 52, 53
 - zebu 52
- Dominance
 - bovid 44
 - Bovinae 49
 - bushbuck 74, 75
 - eland 82, 134
 - gerenuk 432, 436
 - Grant's gazelle 416, 419
 - greater kudu 117, 118
 - hartebeest 516
 - impala 463, 464, 467, 472
 - kudu 82
 - oryx 580, 581, 585

roan antelope 574
sable antelope 563
tommy 405, 406
tragelaphine 74, 75
waterbuck 388

Drinking

dik-dik 252

Drought, survival in
eland 129

E

Ecological niche

alcelaphine 453, 454
Antilopini 396
bongo 79
bovid 2 *et seq.*
bushbuck 78
Caprini 588, 589
hippotragine 541, 543
impala 469
lesser kudu 108
Syncerus c. caffer 64
tragelaphine 78

Ecology

bovid 2 *et seq.*
giant kudu 79, 80

Economics 641 *et seq.*

Bos 52 *et seq.*
bovid 1 *et seq.*
gnu 536, 537
hartebeest 523
kob 381
puku 383
Reduncini 341

Energy budget

bovid 2 *et seq.*

Energy conservation

buffalo 64

Evolution

Alcelaphini 438 *et seq.*
antelope 12 *et seq.*
Antilopini 394 *et seq.*
boselaphine 78
bovid 2 *et seq.*
Bovini 50
Caprini 588
cattle 2
dik-dik 246 *et seq.*
duiker 264 *et seq.*
eland 80, 123, 125
goat 2
Hippotragini 539 *et seq.*
impala 462 *et seq.*

Pelorovis 52
Reduncini 328 *et seq.*
ruminant 5
sheep 2
sitatunga 85, 86
Syncerus 52
caffer 61
tragelaphine 78, 79
Tragelaphini 50
Ugandax 52

Evolutionary status

duiker 170, 264

Excretion

klipspringer 237

Eye socket protrusion

bay duiker 26
Cephalophus dorsalis 316
Oreotragus 27

Eyes

Alcelaphus 31
Antilopini 31
Cephalophus dorsalis 316
Hippotragini 31

F

Facial markings

tragelaphine 31, 32

Family behaviour

buffalo 65, 68

Feeding behaviour

alcelaphine 454, 455
bay duiker 316, 317
buffalo 64
dik-dik 252
duiker 267, 268
eland 127, 129
Gazella granti 398
gerenuk 427, 434, 435
greater kudu 117
hippotragine 548
sitatunga 87
steinbuck 210
sun 196

Fighting

Aepyceros 448
Alcelaphini 444
Alcelaphus buselaphus cokei 444
lelwel 446
antelope 31
Antilopinae 159 *et seq.*
bohor reedbuck 336
bovid 28 *et seq.*
buffalo 29

- buffalo, Cape 60 *et seq.*
- bush duiker 324
- bushbuck 101, 102
- damalisc 29
- Damaliscus lunatus* 448, 496
- dik-dik 257, 258
- duiker 272
- eland 82, 133, 134, 137
- gerenuk 29, 430, 431
- gnu 29, 528, 529
- goat 29
- Grant's gazelle 29, 400, 419, 420
- greater kudu 118, 120
- hartebeest 29, 514, 516
- hirola 477
- impala 473
- klipspringer 241
- kob 377
- kudu 82
- lesser kudu 111
- oryx 29, 580, 581
- Reduncini 335, 336, 337
- roan antelope 573, 574
- sable antelope 29, 563, 564
- sheep 29
- sitatunga 89
- Soemmering's gazelle 424
- southern reedbuck 363, 364
- sun 198
- Thomson's gazelle 29, 400, 410
- waterbuck 29, 389, 390, 391
- Foetus
 - Madoqua* 260
 - Syncerus caffer* 70
- Foraging 49
 - bushbuck 97
 - eland 82, 127
 - greater kudu 82, 117
- Fossil record
 - boselaphine 78
 - bovid 2 *et seq.*
 - Caprini 588
 - gazelle 394
 - greater kudu 79
 - hirola 477
 - impala 464
 - sitatunga 86
 - Syncerus* 60
 - tragelaphine 78
- Frontal sinus 14
 - Alcelaphini 439, 440
 - Caprini 590, 591
 - Rupicaprini 590
- Frontal tuft
 - eland 127, 134, 135
- G
- Gait
 - Alcelaphini 438
 - blue duiker 283
 - bohor reedbuck 356, 357
 - bush duiker 320
 - bushbuck 99
 - eland 82
 - gnu 529
 - hartebeest 505
 - hippotragine 548
 - impala 464, 465, 466
 - klipspringer 231
 - lesser kudu 111
 - Natal red duiker 295
 - oribi 226, 227, 228
 - oryx 579
 - pigmy antelope 191
 - Sharpe's grysbok 205, 206
 - sitatunga 89
 - Soemmering's gazelle 424
 - southern reedbuck 362
 - steinbuck 211, 212
 - tommy 406, 407
 - topi 497
 - tragelaphine 72, 82
- Gestation
 - blue duiker 285
 - bohor reedbuck 358
 - bongo 155
 - buffalo 70
 - bush duiker 326
 - bushbuck 103
 - dik-dik 260
 - eland 137
 - gnu 536
 - Grant's gazelle 420
 - greater kudu 120
 - hartebeest 520
 - hippotragine 548
 - impala 474
 - klipspringer 239
 - kob 380
 - lesser kudu 112
 - mountain reedbuck 348
 - oribi 228
 - oryx 585
 - pigmy antelope 191
 - Reduncini 341
 - roan antelope 576

- sitatunga 93
- Soemmering's gazelle 424
- southern reedbuck 365
- steinbuck 215
- sunī 199
- Thomson's gazelle 410
- topi 500
- yellow-backed duiker 313
- Glands
 - antelope 9
 - bovid 4
 - eland 135
 - oribi 218
- Glands, ear 338
 - bohor reedbuck 358
 - oribi 218, 337
- Glands, facial
 - alcelaphine 450
 - antelopine 48, 49
 - bovine 48, 49
 - bush duiker 325
 - duiker 271
 - hirola 481
 - impala 463
 - oribi 228
 - puku 336
 - steinbuck 213
 - sunī 199, 200
 - topi 496
- Glands, fetlock
 - impala 464, 465
- Glands, inguinal
 - bushbuck 99, 102
 - oribi 218
 - reedbuck 338, 339
 - sitatunga 89
 - southern reedbuck 362, 365
- Glands, pedal
 - alcelaphine 449
 - Antilopinae 12, 48, 49
 - Bovinae 12
 - hippotragine 548
 - oribi 218, 223
 - Reduncini 333
 - sunī 196, 197, 200
 - topi 494
- Glands, preorbital
 - alcelaphine 450
 - bush duiker 324
 - Cephalophini 266
 - dik-dik 177, 255
 - klipspringer 177, 239
 - Madoqua* 177
 - neotragine 177
 - Neotragini 266
 - Neotragus batesi* 266
 - moschatus* 177
 - pygmaeus* 266
 - Oreotragus* 177
 - oribi 24, 25, 177, 181, 218, 223
 - Ourebia* 177
 - pigmy antelope 190
 - reduncine 25
 - Reduncini 333
 - steinbuck 214
 - sunī 177, 193
 - tommy 409
 - topi 495
- Grooming
 - blue duiker 283
 - bush duiker 326
 - Cephalophus maxwelli* 271
 - duiker 271
 - klipspringer 237
 - sunī 196
- Growth rate
 - mountain reedbuck 348
- Habitat
 - Abbot's duiker 307
 - antelope 21
 - bay duiker 317
 - black fronted duiker 303
 - blue duiker 282, 317
 - bohor reedbuck 351, 353
 - bongo 144, 145
 - Bovidae 21
 - buffalo 57, 64
 - bush duiker 320, 321
 - bushbuck 95, 97, 101
 - Cephalophus adersi* 274, 287, 288, 295
 - natalensis* 274, 295
 - rubidus* 274, 292, 293, 295
 - rufigilatus* 274, 291, 295
 - zebra* 274, 295
 - common eland 128
 - Derby's eland 125, 128
 - dik-dik 251
 - duiker 21, 264, 268, 274 *et seq.*
 - eland 81, 82
 - gerenuk 434
 - gnu 525, 527
 - Grant's gazelle 400, 416, 417
 - greater kudu 115, 116
 - hartebeest 509, 510, 512
 - hippotragine 543 *et seq.*
 - hirola 481

impala 461, 462, 468
 klipspringer 231, 234, 236
 kob 367, 368, 378
 kudu 80 *et seq.*
 lechwe 332
 lesser kudu 107, 108
Madoqua guentheri 246
 kirkii 246
 saltiana 246
Neotragus batesi harrisoni 188
 oribi 217, 220, 221
 oryx 582
 Peter's duiker 305, 317
 pigmy antelope 187, 188
 puku 383
Redunca fulvorufula 332, 343, 345
 Reduncini 328 *et seq.*
 roan antelope 569, 571
 sable antelope 556, 557, 558
 Sharpe's grysbok 205
 sitatunga 86, 90
 Soemmering's gazelle 423
 southern reedbuck 361, 362
 steinbuck 209
 suni 194
Syncerus 64
 Thomson's gazelle 400, 403, 405
 topi 485, 488 *et seq.*
 tragelaphine 78, 79
Tragelaphus strepsiceros grandis 79
 white bellied duiker 289
 yellow-backed duiker 309

H

Habitat distribution
 Bovidae 21
 Hair
 klipspringer 231
 Head
 buffalo, forest 57
 savanna 57
Cephalophus dorsalis 315
 nigrifrons 267
 kivuensis 302
 sylvicultor 315
 dik-dik 250, 251
Gazella granti 400
 thomsoni 399, 401, 411
 gerenuk 397
 gnu 453, 532
 hartebeest 166, 441
 hirola 476
 kob 370

lesser kudu 72
Madoqua guentheri 244, 259
 kirkii 244, 249
 saltiana 244
Oryx gazella beisa 545
Ourebia 24
Pelea 24
Redunca fulvorufula 24, 329, 342
 sable antelope 560, 561
 Sharpe's grysbok 203
 steinbuck 211
 suni 193
Syncerus caffer 56
Taurotragus 48
 oryx 135
 Thomson's gazelle 158
 topi 484, 492, 498
 waterbuck 384
 Head flagging
 eland 134
 Grant's gazelle 33
 kudu 33
 Hearing
 eland 127
 Hierachy
 Antilopinae 48 *et seq.*
 bongo 150
 buffalo 67, 68
 Cape 62
 bushbuck 101, 102
 caprine 590
 eland 132, 133, 134
 hartebeest 516
 impala 463 *et seq.*
 Reduncini 333, 340
 sable antelope 555, 563
 southern reedbuck 363
 topi 491
 tragelaphine 75
 Home range
 Antilopinae 171
 bohor reedbuck 354, 356
 bongo 144, 149
 buffalo 65, 66
 bush duiker 171
 bushbuck 100, 101
 common eland 128 *et seq.*
 duiker 270, 272
 eland 82
 gerenuk 171
 Grant's gazelle 418, 419
 greater kudu 82, 117, 118
 hartebeest 512, 516

- hippotragine 543
- impala 469
- kob 369 *et seq.*
- lesser kudu 107, 108, 110
- Madoqua* 171
- mountain reedbuck 171, 346, 347
- Neotragus* 171
- Oreotragus* 171
- oribi 171, 223
- pigmy antelope 187, 188
- Reduncini 333
- roan antelope 569, 571
- sable antelope 555 *et seq.*
- sitatunga 88, 91, 93
- southern reedbuck 362, 363
- steinbuck 213
- tommy 405, 409
- topi 491
- waterbuck 388 *et seq.*
- Hoof
 - gnu 458
 - kongoni 458
 - oryx 583
 - Redunca redunca* 328
 - Syncerus caffer* 60
 - topi 458
- Horn boss
 - buffalo, Cape 57, 61, 62, 71
 - Gazella soemmeringii* 424
 - thomsoni* 424
- Horns
 - Aepyceros* 440
 - melampus* 460
 - Alcelaphini 162, 438 *et seq.*
 - Alcelaphus* 169
 - buselaphus* 443, 446
 - buselaphus* 443, 444
 - caama* 443, 444
 - cokii* 443, 444
 - lelwel* 443, 444, 447, 503
 - lichtensteini* 443, 446, 447
 - major* 443, 444, 446, 447
 - swaynei* 443, 444
 - tora* 443, 444
 - Ammodorcas* 164
 - antelope 9, 12 *et seq.*
 - Antilopinae 12 *et seq.*, 159 *et seq.*
 - Antilopini 398
 - Beatragus hunteri* 439 *et seq.* 476, 473
 - bongo 32, 43, 75
 - bovid 4 *et seq.*
 - Bovinae 12 *et seq.*
 - Bovini 50
 - buffalo, African 57 *et seq.*
 - bushbuck 32, 75, 103
 - Capé rhebok 160
 - Capra falconeri* 77
 - caprine 590
 - Caprini 162, 163
 - Cephalophus adersi* 266, 286
 - callipygus* 304
 - dorsalis* 314, 315
 - harveyi* 296
 - leucogaster* 289
 - monticola* 280
 - natalensis* 294
 - nigrifrons* 300
 - rubidus* 292
 - rufilatus* 290
 - spadix* 306
 - sylvicultor* 308, 312
 - cervid 27
 - chevrotain 27
 - chousingha 50, 77
 - Connochaetes* 169
 - taurinus* 524
 - Damaliscus* 169, 442, 443
 - lunatus* 484
 - Derby's eland 77, 123
 - duiker 160, 266
 - eland 43, 77, 82
 - Eotragus* 12
 - Gazella granti* 398, 415
 - soemmeringii* 422
 - thomsoni* 403, 410
 - gazelline 14 *et seq.*
 - gerenuk 430, 431
 - goat 591
 - Grant's gazelle 31
 - greater kudu 115
 - hippotragine 547
 - Hippotragus* 168
 - equinus* 569
 - niger* 554
 - Hippotragini 162, 163
 - Illingoceros* 78
 - impala 165, 438, 460, 473
 - klipspringer 234
 - Kobus adenota* 329
 - ellipsiprymnus* 329, 384, 385
 - kob 164, 165, 329
 - kob* 331, 367
 - leucotis* 331
 - thomasi* 331
 - leche 329
 - megaceros* 329

vardoni 331, 382 *et seq.*
 kudu 30, 77, 79
 lesser kudu 107
Litocranius walleri 426
Madoqua 14, 15, 162
 guentheri 245
 kirkii 245
 saltiana swaynei 245
Megalotragus 168
Mesembriportax 77, 78
Muntiacus 27
Neotragus 160, 162, 265, 266
 pygmaeus 266
 nilghai 50
Oreotragus 27
 oribi 24, 218
 oryx 31, 169
Oryx gazella 579
Parmularius 443
Pelea 24
 capreolus 160
 pigmy antelope 186
 prongbuck 50
Prototragocerus labidotus 78
Rabaticeros 440, 443
Redunca arundinum 329, 361
 fulvorufula 329
 redunca 25, 329, 342, 350
 bohor 331
 cottoni 331, 350, 356
 nigeriensis 331
 redunca 331
 wardi 331, 350
 Reduncini 162, 163, 333 *et seq.*
 reedbuck 336, 337
 sable 31, 163
 Sharpe's grysbok 202
 sheep 591
 sitatunga 32, 75, 85, 90, 93
 steinbuck 209, 214
 suni 192
Sylvicapra grimmia 319
Taurotragus derbianus 79
 oryx 77, 123, 127, 138
Tetracerus 77
Tetrameryx 78
 tragelaphine 29, 74 *et seq.*
 Tragelaphini 50
Tragelaphus 50, 51
 gaudreyi 79
 grandis 79, 80
 imberbis 79
 nakuae 79

strepsiceros 79
Ugandax 60
 waterbuck 31
 Horn growth
 Alcelaphus buselaphus cokei 506
 lelwel 506
 Antilopinae 162, 163
 bongo 75
 bovid 30
 bushbuck 103
 eland 137
 gnu 530
 greater kudu 120
 kob 380
 tragelaphine 75
 Hybridization
 Alcelaphus buselaphus cokei 503
 lelwel 503
 lichtensteini 503
 Cephalophus 278
 callipygus × *C. harveyi* 305
 dorsalis 317
 dorsalis × *C. zebra* 278
 harveyi × *C. natalensis* 305
 nigrifrons kivuensis 292
 rubidus 292
 zebra 317
 kob 380
Kobus defassa 380
 megaceros 380
 lesser kudu 113
 sitatunga × bushbuck 85
Syncerus c. caffer × *S. c. nanus* 56 *et seq.*
 mathewsi 63
 tragelaphine 83
 Hypsodonty
 Aegodonta 14
 Boodonta 14
 bovid 7
 buffalo 7
 oribi 16
 Redunca fulvorufula 25
 Reduncini 17

 I
 Introduction
 water buffalo 55

 J
 Jaw (*see also* Mandible)
 bovid 23
 buffalo 7
 bushbuck 7

Joints, condylar surfaces 51
Jumps, reedbuck 35
Juvenile behaviour 37

K

Keratin 29, 30
Keratohyalin 29
Knee movements 35, 37, 580

L

Local names

Aepyceros melampus 460
Alcelaphus buselaphus 502
Beatragus hunteri 476
Boocercus eurycerus 142
Cephalophus adersi 286
callipygus 304
dorsalis 314
harveyi 296
leucogaster 289
monticola 280
natalensis 294
nigrifrons 300
rubidus 292
rufilatus 290
spadix 306
sylvicultor 308
Connochaetes taurinus 524
Damaliscus lunatus 484
Gazella granti 414
soemmeringii 422
thomsoni 403
Hippotragus equinus 568
niger 554
Kobus ellipsiprymnus 384
kob 366
Litocranius walleri 426
Madoqua 242
Neotragus batesi 186
moschatus 192
Oryx gazella 579
Ourebia ourebi 218
Oreotragus oreotragus 234
Raphicerus campestris 208
harpei 202
Redunca arundinum 361
fulvorufula 342
redunca 350
Sylvicapra grimmia 318
Syncerus c. caffer 56
Taurotragus derbianus 122
oryx 126
Tragelaphus imberbis 106

scriptus 94
spekei 84
strepsiceros 115

Longevity

blue duiker 285
bohor reedbuck 359
bush duiker 327
duiker 273
gnu 531
oribi 228
yellow backed duiker 313

M

Mammæ

Antilopinae 12
Bovinae 12
Grant's gazelle 415

Mandible

buffalo 7
bushbuck 7

Measurements

Aepyceros melampus 460
Alcelaphus 448
buselaphus 503
Beatragus hunteri 476
Boocercus eurycerus 142
Cephalophus adersi 286
callipygus 304
dorsalis 314
harveyi 296
leucogaster 289
monticola 280
natalensis 294
nigrifrons 300
rubidus 292
rufilatus 290
spadix 306
sylvicultor 308
Connochaetes 448
taurinus 524
Damaliscus lunatus 448, 484
Gazella granti 415
soemmeringii 422
thomsoni 403
Hippotragus equinus 569
niger 554
Kobus ellipsiprymnus 384
kob 367
vardoni 382
Litocranius walleri 426
Madoqua guentheri 245
kirkii 245
saltiana swaynei 245

- Neotragus batesi* 186
moschatus 192
Oreotragus oreotragus 234
Oryx gazella 579
Ourebia ourebi 218
Raphicerus campestris 209
sharpai 202
Redunca arundinum 361
fulvorufula 342
redunca 350
Sylvicapra grimmia 319
Syncerus c. caffer 57
nanus 57
Taurotragus derbianus 122
oryx 126
Tragelaphus imberbis 106
scriptus 94
spekei 84
strepsiceros 115
- Morphology
- Aepyceros melampus* 460, 461
 Alcelaphini 450
Alcelaphus buselaphus lelwel 502
lichtensteini 504, 505
Beatragus hunteri 477, 478
Boocerus eurycerus 142, 143
Bos 50
Boselaphus 49, 50
 Bovini 52,
 buffalo 43
 Caprini 589, 590, 591
Cephalophus adersi 286, 287
callipygus 304, 305
lestradei 305
weynsi 305
dorsalis 314, 315
harveyi 296, 297
leucogaster 289
monticola 280, 282
natalensis 294, 295
nigrifrons 300
fosteri 301
hooki 301
kivuensis 292, 301
rubidus 292
rufilatus 290
spadix 306, 307
sylvicultor 309, 310
Connochaetes taurinus 524, 525
Damaliscus lunatus 487
 dik-dik 251
 duiker 274 *et seq.*
Gazella granti 395, 401, 414, 415
soemmeringii 422, 423
thomsoni 401, 402, 403
 greater kudu 76, 114, 115
Hippotragus equinus 568, 569
niger 538, 552, 554, 555
Kobus ellipsiprymnus 385
kob 366, 367
vardoni 382, 383
Litocranius 50
walleri 426, 427
Madoqua guentheri 243
kirkii 256
Neotragus batesi 186, 187
moschatus 192, 193
Oreotragus oreotragus 231 *et seq.*
Oryx gazella 578, 579
Ourebia ourebi 217, 219
Raphicerus campestris 203, 204, 208,
 209
sharpai 202, 203
Redunca arundinum 360, 361
fulvorufula 343, 344
redunca 351, 352
 Sharpe's grysbok 202, 203, 204
Sylvicapra grimmia 318, 319, 320
deserti 319
nyansae 319
orbicularis 319
roosevelti 319
Syncerus c. caffer 56
caffer × *S. c. nanus* 58
 suni 43, 192, 193
Taurotragus derbianus 122, 123
oryx 123, 126, 127, 138
Tetracerus 49, 50
 tragelaphine 72
Tragelaphus imberbis 72, 73, 106, 107
scriptus 94, 95
spekei 84, 85
strepsiceros 115
- Mortality
- Alcelaphus buselaphus cokei* 522
 bohor reedbuck 358
 bongo 155, 156
 buffalo 69, 70
 bushbuck 105
 dik-dik 261
 eland 138
 gnu 530, 533 *et seq.*
 hartebeest 521
 hippotragine 547
 impala 474
 klipspringer 241

oryx 585
 puku 383
 sable antelope 566
 Thomson's gazelle 411
 tragelaphine 74
 waterbuck 391, 393
 Mortality causes
 Abbotts duiker 307
 alcelaphine 459
 Alcelaphus buselaphus cokei 522
 black fronted duiker 303
 bohor reedbuck 358
 bongo 145, 155
 buffalo 70, 71
 bush duiker 322
 bushbuck 104, 105
 dik-dik 261
 eland 138, 139
 Gazella granti 399, 420
 thomsoni 398, 411, 412, 413
 gnu, 527, 530 *et seq.*
 greater kudu 121
 hartebeest 521, 522
 hirola 482
 impala 473, 474
 klipspringer 241
 kob 381
 lesser kudu 113
 mountain reedbuck 347, 348
 oribi 222, 228
 oryx 585, 586, 587
 Peter's duiker 305
 pigmy antelope 191
 roan antelope 576
 sable antelope 566
 Sharpe's grysbok 207
 sitatunga 90
 southern reedbuck 364
 suni 201
 topi 489 *et seq.*
 waterbuck 391
 yellow-backed duiker 312
 Muscle, longus capitis
 gerenuk 431
 kob 337
 mountain reedbuck 337
 oribi 337
 Reduncini 337
 Muscle, masticatory
 antelope 23
 bovid 23 *et seq.*
 Cephalophus dorsalis 26
 oribi 23 *et seq.*

Pelea capreolus 23 *et seq.*
Redunca fulvorufula 23 *et seq.*
Tragelaphus scriptus 23
 Musculature
 Alcelaphus buselaphus lelwel 445
 Beatragus 439
 bongo 156
 bushbuck 105
 Cephalophus monticola 263
 sylvicultor 311
 Damaliscus lunatus 498
 eland 82
 Gazella granti 394
 gerenuk 429, 430, 431
 gnu 528
 hirola 479
 klipspringer 233
 Kobus ellipsiprymnus 334
 Madoqua guentheri 242
 Neotragus batesi 179
 moschatus 180
 oryx 550
 Ourebia 181
 Redunca redunca 340
 sable antelope 553, 561
 steinbuck 212
 Syncerus c. caffer × *S. c. nanus* 59
 Taurotragus oryx 132
 tommy 408
 topi 486
 tragelaphine 82

N

Nose
 dik-dik 246, 249
 hartebeest 458
 Madoqua guentheri 245
 kirkii 245
 saltiana 245
 Nucleic acid/nitrogen metabolism
 ruminant 5

O

Olfaction
 blue duiker 283
 oribi 22

P

Parallelism
 bovid 7
 Parasites (*see* Diseases and parasites)
 Phylogeny
 Antilopinae 12 *et seq.*, 159, 170

- Antilopini 170, 171
- Boselaphini 9
- Boselaphus* 9, 50
- bovid 2 *et seq.*
- Bovinae 12, 50
- Bovini 9, 50
- Cephalophini 169
- chousingha 50
- Hippotragini 539 *et seq.*
- neotragine 50
- Raphicerus* 169
- Reduncini 328
- ruminant 5
- sitatunga 85, 86
- Tetracerus* 50
- Tragelaphini 9, 50, 78
- Physiology
 - bovid 8
 - eland 129
- Play
 - bushbuck 103
 - southern reedbuck 365
 - waterbuck 393
- Population density
 - alcelaphine 455
 - bohor reedbuck 354 *et seq.*
 - bongo 152, 154
 - buffalo 69
 - bush duiker 321
 - bushbuck 44, 100
 - Cephalophus callipygus* 317
 - dorsalis* 317
 - monticola* 317
 - Connochaetes* 452, 453
 - Derby's eland 125
 - Gazella granti* 398
 - thomsoni* 398, 405
 - gerenuk 436
 - gnu 44
 - greater kudu 118
 - hartebeest 512, 513, 514, 530
 - hirola 480, 481
 - hippotragine 546
 - impala 44, 470, 471
 - klipspringer 236
 - kob 44, 369, *et seq.*
 - mountain reedbuck 347
 - oribi 221, 222
 - Oryx* 546
 - pigmy antelope 189, 190
 - Redunca r. cottoni* 356
 - Reduncini 331 *et seq.*
 - roan antelope 570, 571
 - sable antelope 547
 - sitatunga 44, 88
 - Soemmering's gazelle 424
 - southern reedbuck 363
 - topi 44, 491 *et seq.*
 - waterbuck 391
- Predators
 - blesbok 498
 - blue duiker 283, 284
 - bohor reedbuck 358
 - bongo 155
 - buffalo 68 *et seq.*
 - bush duiker 326
 - bushbuck 103, 104
 - dik-dik 253
 - duiker 273
 - eland 138, 139
 - Gazella granti* 398, 399, 420, 421
 - thomsoni* 398, 399, 412, 413
 - gnu 533, 534, 535
 - greater kudu 121
 - hartebeest 521, 522
 - hippotragine 544, 545, 546
 - Hippotragus* 544
 - hirola 482
 - impala 473, 474
 - klipspringer 231, 241
 - kob 371, 381
 - lesser kudu 112
 - mountain reedbuck 347
 - oribi 222
 - oryx 585, 586
 - Peter's duiker 305
 - pigmy antelope 191
 - roan antelope 571, 576
 - sable antelope 566
 - sitatunga 89, 90
 - southern reedbuck 364
 - steinbuck 215
 - topi 497, 498, 499
 - tragelaphine 74
 - waterbuck 391, 392
- Pronking 37
 - bovid 37
 - damalisc 37
 - Dolichotis* 37
 - gazelle 37
 - hartebeest 37
 - Rhynchocyon* 37
 - southern reedbuck 362
 - tommy 407

R

Radiation

- antelope 21
- Antilopinae 8 *et seq.*
- boselaphine 17
- bovid 8 *et seq.*
- Bovinae 8 *et seq.*
- caprid 14
- Caprini 589, 590
- dik-dik 245 *et seq.*
- duiker 20, 21, 263 *et seq.*, 274 *et seq.*
- eotragine 17
- Gazella* 398
- hippotragine 540
- neotragine 17, 172 *et seq.*
- sitatunga 85, 86
- tragelaphine 78

Reproductive behaviour

- alcelaphine 457, 458, 459
- blue duiker 284
- bohor reedbuck 358
- bongo 155
- buffalo 66 *et seq.*
- bushbuck 102
- dik-dik 254, 258
- gnu 536
- Grant's gazelle 420
- hartebeest 513, 514
- hippotragine 548, 549
- hirola 482
- impala 466, 467, 471, 474
- klipspringer 239, 240
- kob 380, 381
- mountain reedbuck 348
- oribi 182, 228
- oryx 585
- puku 383
- Reduncini 340
- roan antelope 575
- sable antelope 561
- sitatunga 93
- Soemmering's gazelle 424, 425
- southern reedbuck 364
- steinbuck 215
- sun 199
- Thomson's gazelle 410, 411
- topi 494, 499
- waterbuck 392, 393
- yellow-backed duiker 313

Rumen

- bovid 3 *et seq.*

Rumination

- alcelaphine 454

bovid 4 *et seq.*

dik-dik 253

S

Scent marking (*see* Communication, scent)

'Security strategy'

ruminant 3, 6

Sex ratio

- bushbuck 103
- gnu 530
- greater kudu 118
- hartebeest 515
- klipspringer 237, 241
- pigmy antelope 190
- sable antelope 565
- steinbuck 213
- waterbuck 391

Sexual dimorphism

- blue duiker 284
- bovid 44
- Bovinae 50
- Cape buffalo 57
- steinbuck 213
- tragelaphine 83
- Tragelaphus spekei selousi* 85
- spekei* 85

Sexual maturation

- alcelaphine 459
- big-horn sheep 590
- blue duiker 285
- bongo 155
- buffalo 70
- bush duiker 326
- bushbuck 102
- chamois 590
- dik-dik 261
- gnu 536
- greater kudu 121
- hartebeest 514, 521
- impala 475
- klipspringer 241
- lesser kudu 112
- mountain reedbuck 348
- oribi 182, 229
- roan antelope 575
- sitatunga 93
- steinbuck 215
- sun 199
- Thomson's gazelle 410
- topi 500

Sight

- bushbuck 99, 100

- eland 127
- hippotragine 548
- klipspringer 231
- Site trampling
 - sitatunga 87
- Size
 - Alcelaphini 20, 438
 - antelope 20
 - antidorcine 15
 - antilopine 48, 396
 - bongo 20
 - bovid 8 *et seq.*
 - bovine 48
 - buffalo 8, 9, 20, 57
 - Cephalophus* 274 *et seq.*
 - duiker 8, 9, 20, 264, 270
 - eland 20
 - Gazella granti* 398
 - thomsoni* 398
 - giant kudu 20, 79, 80
 - Kobus adenota* 329
 - ellipsiprymnus* 329
 - kob* 329, 331
 - leche* 329
 - megaceros* 329
 - mountain reedbuck 170, 348
 - Neotragini 20, 170, 172
 - oribi 22
 - Redunca arundinum* 329
 - fulvorufula* 329
 - redunca* 329, 331
 - Reduncini 329, 331
 - sitatunga 85
 - tragelaphine 78
- Skeleton
 - Alcelaphus buselaphus lelwel* 449
- Boocerus eurycerus* 143
- bushbuck 104
- Cephalophus callipygus* 269
- sylvicultor* 311
- gerenuk 428
- gnu 529
- Kobus ellipsiprymnus* 335
- Madoqua saltiana* 258
- Neotragus batesi* 178
- oryx 551
- roan antelope 577
- sable antelope 562
- steinbuck 213
- sun 193
- Syncerus c. caffer* × *S. c. namus* 58
- Taurotragus oryx* 133
- tommy 409
- Tragelaphus strepsiceros* 76
- Skull
 - Alcelaphini 439
 - Alcelaphus* 440
 - buselaphus lelwel* 446
 - lichtensteini* 446, 447
 - major* 446
 - Beatragus* 440
 - beira 172
 - bush duiker 321
 - Cephalophus callipygus* 264
 - dorsalis* 17, 26, 315, 316
 - harveyi* 299
 - leucogaster* 289
 - monticola* 17, 266
 - nigrifrons* 316
 - rufilatus* 291
 - spadix* 307
 - sylvicultor* 312
 - Connochaetes* 440
 - Damaliscus lunatus* 440
 - Dorcotragus* 174
 - duiker 264, 265
 - Eotragus* 174
 - gerenuk 431
 - goat 591
 - hippotragine 540
 - Hippotragus* 541
 - impala 462, 463
 - klipspringer 231
 - Madoqua guentheri* 174
 - kirkii* 174, 258
 - saltiana* 174
 - neotragine 24, 25, 174
 - Neotragini 174
 - Neotragus batesi* 174, 176, 188, 266
 - moschatus* 174, 175, 176, 198
 - pygmaeus* 174, 176
 - Oreotragus* 27
 - oribi 225
 - Oryx* 541
 - Ourebia* 23, 25, 174, 175
 - ox 54
 - Pelea capreolus* 23 *et seq.*
 - Raphicerus campestris* 174, 204
 - melanotis* 174
 - sharpei* 174, 204
 - Redunca fulvorufula* 23 *et seq.*
 - Reduncini 336
 - sheep 591
 - steinbuck 209
 - Social behaviour 49
 - alcelaphine 454 *et seq.*

blue duiker 285
 bohor reedbuck 354 *et seq.*
 bongo 43, 44, 74, 149, 150
 bovid 42
 buffalo 58, 65 *et seq.*
 bush duiker 324 *et seq.*
 bushbuck 97 *et seq.*
Cephalophus maxwelli 283
 dik-dik 254 *et seq.*
 duiker 271
 eland 43, 74, 130 *et seq.*
 gerenuk 432, 436
 gnu 44, 452, 531
 Grant's gazelle 400, 416 *et seq.*
 greater kudu 43, 117, 118
 hartebeest 511 *et seq.*
 hippotragine 547 *et seq.*
 hirola 481 *et seq.*
 impala 462 *et seq.*
 klipspringer 237 *et seq.*
 kob 44, 369 *et seq.*
 lesser kudu 110, 111
 mountain reedbuck 346, *et seq.*
 oribi 223 *et seq.*
 oryx 585
 pigmy antelope 189, 190
 puku 383
 Reduncini 333 *et seq.*
 roan antelope 570 *et seq.*
 sable antelope 547, 548
 Soemmering's gazelle 424
 southern reedbuck 362 *et seq.*
 steinbuck 213
 suni 196, 197
 Thomson's gazelle 400, 405 *et seq.*
 topi 44, 491 *et seq.*
 tragelaphine 43, 74 *et seq.*
 waterbuck 387 *et seq.*
 yellow-backed duiker 312
 Social organization
 Alcelaphini 456 *et seq.*
 Antilopinae 160 *et seq.*
 bovid 4
 buffalo 58 *et seq.*
 bushbuck 97 *et seq.*
 common eland 132, 134
 gerenuk 436
 gnu 527
 Grant's gazelle 416
 lesser kudu 110
 Reduncini 332
 Thomson's gazelle 400, 405
 topi 490

Social unit
 African buffalo 58, 66
 blue duiker 285
 bohor reedbuck 354
 bongo, 150 *et seq.*
 bush duiker 324
 bushbuck 97, 99, 101
 Cephalophus maxwelli 283
 common eland 129, 130
 Derby's eland 125
 dik-dik 254
 duiker 272
 gnu 530
 Grant's gazelle 416, 418
 hartebeest 511, 516
 hirola 481
 impala 469 *et seq.*
 klipspringer 236
 kob 370 *et seq.*
 lesser kudu 110
 mountain reedbuck 346
 oribi 223
 oryx 583, 585
 puku 383
 roan antelope 570, 573
 sitatunga 88, 89
 Soemmering's gazelle 424
 southern reedbuck 340, 364
 suni 197
 tommy 405
 topi 491 *et seq.*
 waterbuck 340, 387
 Socialization
 bushbuck 103
 eland 139
 Specialization
 Antilopini 394 *et seq.*
 bovid 3 *et seq.*
 Caprini 589
 Madoqua guentheri 245
 kirikii 245
 saltiana 245
 Reduncini 328 *et seq.*
 Speciation
 bovid 7
 Cephalophus 298, 299
 duiker 7, 264 *et seq.*
 Stomach
 hartebeest 22
 lesser kudu 22
 oribi 22
 ruminant 5
 suni 22

Stotting 37
 tommy 406, 407
 Stripes
 bushbuck 95
 sitatunga 85
 Survival
 greater kudu 121
 sitatunga 90
 Swimming
 blue duiker 282
 sitatunga 87
 Symbolism
 buffalo 71
 greater kudu 121

T

Taming
 eland 139
 sitatunga 91
 Teeth (*see* Dentition)
 Territorial behaviour
 alcelaphine 5, 455 *et seq.*
Alcelaphus buselaphus 45
 antelope 9, 33
 black fronted duiker 302
 blue duiker 285
 bohor reedbuck 354 *et seq.*
 bovid 4, 5, 33, 44 *et seq.*
 bush duiker 324
 caprine 590
Cephalophus maxwelli 283
 dik-dik 35, 178, 179, 183, 253 *et seq.*
 duiker 33, 270
 gerenuk 436
 gnu 452, 527 *et seq.*
 Grant's gazelle 416 *et seq.*
 grysbok 35
 hartebeest 511 *et seq.*
 hippotragine 543
 hirola 481, 482
 impala 35, 463, 466 *et seq.*
 kob 369 *et seq.*
 mountain reedbuck 346, 347, 348
 neotragine 33
 oribi 181, 182, 221 *et seq.*
 pigmy antelope 190
 puku 383
 Reduncini 333
 reedbuck 33, 35
 roan antelope 570 *et seq.*
 sable antelope 555 *et seq.*
 Sharpe's grysbok 206

Soemmering's gazelle 424
 southern reedbuck 362 *et seq.*
 steinbuck 214, 215
 suni 183, 196 *et seq.*
 tommy 405 *et seq.*
 topi 491 *et seq.*
 tragelaphine 33, 73, 74
 waterbuck 385 *et seq.*
 yellow backed duiker 312
 Thermoregulation
 Antilopinae 12
 Bovinae 12
 dik-dik 172, 249, 250
Gazella granti 398, 403
thomsoni 398, 403
 klipspringer 234
 Neotragini 172
 oryx 586
 reedbuck 354
Saiga tartarica 249
 Toothrow (*see* Dentition)
 'Tournament'
 oryx 580, 581
 Use by man (*see also* Economics) 641
et seq.
 bohor reedbuck 359
 bush duiker 326, 327
 bushbuck 105
Cephalophus monticola 285
rubidus 293
 eland 141
 gnu 537
 Grant's gazelle 421
 greater kudu 121
 oryx 587
 sitatunga 90
 tommy 413

V

Variation
 African buffalo 62, 63
Syncerus caffer brachyceros 63
Tragelaphus scriptus 95 *et seq.*

W

Water loss
 alcelaphine 12
 antelope 12
 antilopine 12
 dik-dik 249, 250
 eland 12

hippotragine 12
 waterbuck 12
 zebu 12
 Weight
Aepyceros melampus 460
Alcelaphus buselaphus 503
Beatragus hunteri 476
Boocercus eurycerus 142
 bovid 19, 20
 bushbuck 83
Cephalophus adersi 286, 287
callipygus 304
dorsalis 314
harveyi 296
leucogaster 289
monticola 280
natalensis 294
nigrifrons 300
rubidus 292
rufilatus 290
spadix 306
sylvicultor 308
Connochaetes taurinus 524
Damaliscus lunatus 484
 eland 82, 83
Gazella granti 415
soemmeringii 422
thomsoni 403
Hippotragus equinus 569
niger 554
Kobus ellipsiprymnus 384
kob 367
vardoni 382
 kudu 82, 83
Litocranius walleri 426
Madoqua guentheri 245
kirkii 245
saltiana swaynei 245
Neotragus batesi 186
moschatus 192
Oreotragus oreotragus 234
Oryx gazella 579
Ourebia ourebi 218
Raphicerus campestris 209
sharpai 202
Redunca arundinum 361
fulvorufula 342
redunca 350
cottoni 350
wardi 350
Sylvicapra grimmia 319
Syncerus caffer 57
Taurotragus derbianus 122

oryx 126, 127
Tragelaphus imberbis 106
scriptus 94
spekei 84
strepsiceros 115

Y

Young

alcelaphine 458, 459
 blue duiker 285
 bohor reedbuck 359
 bongo 155
 bush duiker 326
 bushbuck 103
 dik-dik 260, 261
 duiker 272
 eland 130, 138
 gerenuk 437
 gnu 536
 Grant's gazelle 420
 greater kudu 121
 hartebeest 521
 hippotragine 548
 hirola 482
 impala 474, 475
 klipspringer 240, 241
 kob 381
 mountain reedbuck 348
 oribi 229
 oryx 585
 Reduncini 341
 roan antelope 576
 sable antelope 565, 566
 Sharpe's grysbok 207
 sitatunga 89, 93
 southern reedbuck 365
 steinbuck 215
 suni 199, 200
 Thomson's gazelle 410, 411
 topi 500
 waterbuck 387, 393
 yellow-backed duiker 313

Young, care of

alcelaphine 459
 blue duiker 285
 bohor reedbuck 359
 bush duiker 285
Cephalophus natalensis 273
 dik-dik 260
 gerenuk 437
 gnu 536
 Grant's gazelle 420, 421
 hartebeest 514, 521

hippotragine 549
impala 474
kob 381
Reduncini 341
sable antelope 566

southern reedbuck 365
suni 200
Thomson's gazelle 410, 411
topi 500
waterbuck 393

**The Role of Visual Signals
and Face Patterns in
African Forest Monkeys
(Guenons) of the Genus
*Cercopithecus***

J. S. Kingdon

This paper explores the evolutionary origins of facial patterns in a single closely related genus of African monkeys. It sets out to identify the major factors that determine pattern formation and demonstrate the apparent role of facial signal patterns in the monkey's communication systems.

The mechanics of pattern elaboration are demonstrated through detailed examination of hair and skin pigmentation in closely related species. The effects of species-specific communication systems are sought in their distribution and evidence is presented for face patterns providing a mechanism that reinforces genetic isolation.

This paper has an entirely new and ecologically based approach to the problem of analysing optical communication and the evolution of signal devices in animals and more specifically in Old World simian primates. At a general level this paper is an essay exemplifying the role of patterns in animal communication and will be of interest to biologists, primatologists, naturalists and students of communication.

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